FORESTRY

FOREST RESOURCE DEVELOPMENT AGREEMENT

Canada

BC

92-04399/

FRDA REPORT 034

THE INFLUENCE OF SITE QUALITY ON TREE RESOURCE ALLOCATION TO FINE ROOTS AND ITS EFFECT ON HARVESTABLE PRODUCTIVITY OF COASTAL DOUGLAS-FIR STANDS

BY

WERNER A. KURZ AND J.P. KIMMINS*

*Faculty of Forestry
The University of British Columbia
2357 Main Mall
Vancouver, B.C.
V6T 1W5

Report to the Canadian Forestry Service
Pacific & Yukon Region
506 W. Burnside Road
Victoria, B.C. V8Z 1M5
Scientific authority: Dr. Holger Brix
FRDA Contribution Agreement: 68576-52-6-2

April, 1987

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ISSN 0835-0752

ABSTRACT

The main objectives of the study presented in this report were to establish the seasonal pattern of live fine root biomass in second-growth coastal Douglas-fir stands of five different site qualities, and to quantify annual fine root production in these stands. Root samples for this study were collected on 6 sampling dates from May 1985 to May 1986 in 5 research sites on eastern Vancouver Island, which cover a range of site indices from 25 to 41 m at breast-height age 50 years.

Coniferous ash-free live fine root biomass (0-2 mm diameter) in May 1985 ranged from 182 g/m^2 to 791 g/m^2. The highest fine root density was found in the forest floors which, although less than 2 cm thick, contained 13% to 28% of the fine roots in the top 50 cm of the soil profile.

All five stands displayed a similar pattern in live and dead fine root biomass. Live fine root biomass was highest in May 1985, decreased sharply in August and October, and increased again in the May 1986 samples. Dead fine root biomass displayed the opposite trend: low in May 1985, high in August and October, and decreasing again in May 1986. Annual fine root mortality was 60% to 100% of the live fine root biomass present in May 1985, and in some stands live fine root biomass in May 1986 had only recovered to 50% of the May 1985 value. This suggests large between-year

variation in fine root biomass. Total fine root biomass, i.e. live plus dead, showed very little seasonal change. This emphasizes the need to differentiate root samples into live and dead categories if seasonal dynamics and fine root production are to be quantified.

When annual fine root production estimates were based on significant changes in live fine root biomass only, values for different sites ranged from 112 g/m^2 to 481 g/m^2, a more than four fold difference. These root dry weights are equivalent to the weight of 2.5 m^3/ha and 10.7 m^3/ha of stemwood, respectively. Because fine root biomass in May 1986 was lower than in May 1985 in several stands, mortality estimates were higher than production estimates.

The correlation between site index and both fine root production and mortality was always negative, but never significant. Fine root turnover, defined as the ratio of annual production to fine root biomass in May 1985, was always positively correlated with site index, and if the production estimate was based on significant changes in live fine root biomass, the correlation was significant ($p \leq 0.1$).

The effects of site quality on the proportion of total net primary production allocated belowground is currently being investigated in an ongoing research project.

Future research should attempt to identify factors which cause fine root mortality and factors which affect

photosynthate allocation to belowground stand components. The effects of forest management activities, such as thinning and fertilization, on photosynthate partitioning and allocation to belowground biomass components must be understood if forest growth responses to such silvicultural activities are to be predicted.

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ACKNOWLEGDEMENTS

This project would not have been possible without the dedication of several people who spent many months processing and sorting fine root samples. We thank Claire Trethewey and Ray Morello for their patient and reliable assistance throughout the duration of this project. We also thank Patricia Riley, Debra Stowe, Nora Galdert, Shamsah Mohamed, Gordon Weber and Thomas Smith for their assistance in the processing of root samples. The cooperation of Min Tzse, Senior Laboratory Technician of the Forest Ecology Laboratory at the University of British Columbia, was much appreciated. Ann McGee provided some line drawings and reviewed early drafts of this report. Her help was much appreciated.

Financial support for this project was provided by the Canadian Forestry Service FRDA, Direct Delivery Program, Contribution Number 68576-52-6-2. WAK was the recipient of a World University Service of Canada scholarship during part of this project.

1. INTRODUCTION

In the past, both forest management and forest research have focussed primarily on the aboveground portion of forest stands. More recently, awareness of the importance of belowground production and biomass, and their role in carbon and nutrient budgets, has increased. It appears that a large but variable proportion of net annual photosynthate production is allocated to belowground biomass components, especially fine roots (Agren *et al.* 1980, Harris *et al.* 1980, Vogt *et al.* 1983).

Estimates of the proportion of total photosynthate production allocated to fine roots vary between species and with site and stand conditions. Between-stand variation in harvestable forest productivity is attributable to differences in both total production and allocation of production to above- and belowground biomass components. Recent research results (Keyes and Grier 1981, Grier *et al.* 1986) suggest that between-stand differences in allocation account for much of the observed spatial variation in harvestable productivity of a tree species.

The difficulties in obtaining estimates of fine root biomass and turnover in forest ecosystems are refelected in the paucity of available information. Our understanding of production and mortality of belowground biomass components is very limited, particularly when compared to our

understanding of the aboveground components of the same ecosystems. Improved understanding of belowground processes may provide explanations for the differences in stand responses to a variety of forest management activities such as thinning and fertilization. This may lead to the development of yield improvement strategies with the specific objective of increasing the harvest index by reducing photosynthate allocation to fine roots.

The research reported here is part of a Ph.D. research project (Kurz, in prep.), the objective of which is to establish the relationships between foliage biomass, foliage nitrogen capital, and net primary production in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ecosystems which vary in site quality. The specific objective of the work presented here was to establish the seasonal pattern of fine root biomass in second growth Douglas-fir stands of five different site qualities and to quantify annual fine root production in these stands.

The results presented in this report are part of an ecosystem-level study which is still in progress. Several interesting findings will be reported here but the complete picture will only emerge when the remaining parts of this study have been completed. Therefore, answers to some of the points addressed in this report must await the analysis of additional data. The completed Ph.D. dissertation will be available by the end of 1987.

2. LITERATURE REVIEW

2.1 Estimating fine root biomass

The estimation of fine root biomass in forest stands is an extremely time consuming and labour intensive task. The difficulty of obtaining the necessary field data is reflected in the paucity of information about belowground processes in forest ecosystems.

Quantitative estimates of fine root biomass are normally obtained from soil samples taken either as cores (cf. Moir and Bachelard 1969, Vogt *et al.* 1981, Santantonio *et al.* 1977) or in the form of excavated soil blocks (Harris *et al.* 1977, Kimmins and Hawkes 1978). Soil cores generally contain a smaller soil volume, and therefore require less processing time to separate fine roots from the mineral and organic matter. This permits the collection and processing of a larger number of replicate samples.

2.2 Horizontal and vertical distribution of fine roots

Within a site, fine root density (expressed as weight per unit soil volume or as root length per unit soil volume) generally is related to nutrient availability and decreases with increasing soil depth (Persson 1980, 1983). The majority of fine roots is in the upper 50 cm of forest soil

and most of the absorbing roots can be found in the top 20 cm (Hermann 1977, Kimmins and Hawkes 1978, Gislason 1984).

Horizontal variability in the distribution of fine roots within forest stands depends on stand and site conditions. Moir and Bachelard (1969) found no correlation between the total amount of fine roots extracted from the soil cores and the distance of the sampling point to the nearest live stem in a 19-year-old *Pinus radiata* D. Don plantation. Similarly, Santantonio *et al.* (1977) applied a polygon sampling method in an old-growth Douglas-fir forest and found little or no correlation between small root (<10 mm) biomass and distance of the sample point to the centre of sample trees. In contrast, Persson (1980) found that fine root biomass (<2 mm) decreases with increasing distance from the nearest tree in a 15- to 20-year-old *Pinus sylvestris* L. plantation in central Sweden. An effect of sampling position on fine root weight per sample was also observed in a *Picea sitchensis* (Bong.) Carr. plantation which had been ploughed prior to planting in order to reduce water-logging (Ford and Deans 1977).

Horizontal variability of fine root density in closed forest stands is probably determined primarily by heterogeneous soil conditions and not by distance to the nearest tree. It is impossible, however, to determine soil conditions of the sampling location prior to extracting the soil core. Therefore, no *a priori* stratification of the

sampling position should be attempted and sampling points should be selected at random.

2.3 Nutrient availability and fine root biomass

A number of seemingly contradictary observations concerning the relationship between fine root biomass and nutrient availability have been reported in the literature. Many of the hypotheses derived from these observations are not mutually exclusive, but relate to differences in the spatial scale, ranging from microsite to whole-site scales, of the research on which the hypotheses are based.

Plants appear to allocate root growth preferentially to microsites with greater nutrient availability. For example, in a laboratory split-root experiment with Sitka spruce seedlings, one pot was supplied with water and nutrients while the other received water only (Coutts and Philipson 1976; Philipson and Coutts 1977). Root diameters and mass increased in the pot with the greater nutrient availability. Although transfer of nutrients to the roots in the water-only pot occurred, it did not stimulate root growth in that pot.

Several studies have demonstrated the same phenomenon in the field; within one site, fine roots preferentially exploit regions with higher nutrient availability. In

experiments with ingrowth bags containing nutrient poor and nutrient rich substrates, St.John (1983) found that while there was an equal probability that fine roots would enter both types of ingrowth bags, a significantly greater fine root biomass developed in the nutrient rich material. Similarly, Coopersmith (1986) observed 5 to 10 times as much live coniferous fine root biomass in nutrient-enriched ingrowth bags compared with sand or soil filled bags in a coastal Douglas-fir stand on Vancouver Island, British Columbia. Such results have also been reported by Cuevas and Medina (1983) for an Amazon moist forest.

The above examples are concerned with the relationship between root growth and nutrient availability at the microsite level. This relationship can be different when considered at the whole stand level. In a series of laboratory experiments with a number of tree species (Ingestad 1979, 1981, Ingestad and Lund 1979, Ingestad and Kahr 1985) it was observed that increasing nutrient availability to seedlings resulted in greater overall seedling growth, but that the proportion of this increased growth which was allocated to roots decreased. Furthermore, the morphology of fine roots differed: roots in nutrient-poor solutions were longer and possessed fewer side branches (Ingestad and Lund 1979).

Several field fertilization experiments have supported the finding that increased nutrient availability decreases

the proportion of total photosynthate production allocated to fine roots. This does not necessarily imply that fine root biomass is reduced in fertilized plots. In fact, if overall production increases as nutrient availability increases, fine root production and biomass may also increase even if the allocation to fine roots generally becomes proportionately less.

Linder and Axelsson (1982) found both an overall decline in fine root production and a decline in the proportion of photosynthates allocated to fine roots in irrigated and fertilized plots of *Pinus sylvestris* compared with control plots. Grier *et al.* (1986) reported higher fine root biomass (<2mm) in control than in urea-nitrogen fertilized Douglas-fir stands. Nitrogen fertilization in a 35-year-old *Picea sitchensis* plantation resulted in decreased production of mycorrhizae, finest roots (<1mm) and fine roots (1-5mm). However, mortality of these root classes was also reduced by fertilization, and the combined effects led to an increase in mean biomass in each category (Alexander and Fairley 1983). Urea fertilization of coastal western hemlock significantly reduced the number of mycorrhizae and accelerated the rate of mycorrhizal mortality (Gill and Lavender 1983).

To satisfy the tree's nutrient demand it would appear to be necessary to increase fine root surface area as nutrient availability decreases. Comparisons within one

species have shown a greater fine root biomass on poor and dry sites than on rich and moist sites (Keyes and Grier 1981; Santantonio and Hermann 1985; Vogt *et al.* 1983). In contrast, Nadelhoffer *et al.* (1985) report that fine root production increases with greater nitrogen availability. This relationship was confounded, however, with a change in overstory species composition. Their estimates of fine root production were based on a nitrogen budget approach which will be discussed in the next section.

2.4 Estimating fine root production and turnover

There is no direct way to measure fine root production, mortality and decomposition. Consequently, all indirect methods have to invoke a number of assumptions about the observed system. There is no consensus among scientists about the best method of estimating fine root production, but the advantages and disadvantages of some of the methods have been discussed in the literature.

Estimates of fine root production have been derived from a variety of measurements of different ecosystem components and processes, using different computational methods. Methods most commonly used are based on sequential estimates of fine root biomass obtained from soil cores (Moir and Bachelard 1969, Santantonio and Hermann 1985, Vogt

et al. 1980). Other approaches are based on root ingrowth bags (Ericsson and Persson 1980, Coopersmith 1986), observation windows (Keyes and Grier 1981, Bohm 1979), and on the balancing of nitrogen budgets (Nadelhoffer *et al.* 1985). These methods will be discussed below.

Estimates of fine root biomass of an ecosystem are based on destructive samples taken in several locations. Any particular location cannot be sampled more than once. This assumes that differences in observed fine root biomass between two sampling dates are due to production and/or mortality and not to spatial heterogeneity of the system being sampled. Spatial variation of fine root biomass in forest ecosystems is typically high, however, and few (if any) studies use sample sizes sufficiently large to permit an accurate differentiation between sampling error and true seasonal changes in fine root biomass (Vogt *et al.* 1986, Singh *et al.* 1984). The total number of samples that can be taken and processed in a study is generally resticted by the long processing time required for each sample.

Estimates of fine root production and turnover which are based on seasonal dynamics of fine root biomass incorporate several important assumptions (Kurz and Kimmins, in press, Appendix 1 of this report). Production, mortality and disappearance are rate variables (i.e. processes) which are to be derived from the measurements of state variables (i.e. quantities). Each state variable (live and dead fine

root biomass) is determined by two rate variables and changes in the state variable cannot unequivocally be attributed to only one rate variable. For example, live fine root biomass at time t_2 is equal to live fine root biomass at time t_1 plus production minus mortality. Whenever these two processes occur simultaneously, an estimate of one of the rate variables obtained from the observed change in the state variable will be an underestimate.

Seasonal dynamics of fine root biomass and production traditionally have been determined by sequential sampling of fine root biomass. The implicit assumption is that the peaks and troughs in the seasonal pattern coincide with the sampling dates. Failure to capture peaks and troughs will lead to an underestimation of fine root biomass production. Increasing the sampling frequency will increase the probability that all peaks and troughs are included. If the total number of samples which can be processed in a project is restricted, however, an increase in the sampling frequency will reduce the number of samples which can be taken at any one sampling date. This, in turn, will reduce the rsearcher's ability to distinguish "true" changes in fine root biomass from those attributable to random error. Furthermore, if two processes occur simultaneously (e.g. production and mortality), increasing the sampling frequency does not reduce the degree of underestimation in the production estimate. Vogt *et al.* (1986) recommended that

information on root phenology should be used when root sampling protocols are designed.

Several different computational methods have been used to calculate fine root production and mortality from seasonal dynamics in fine root biomass (Persson 1978, McClaugherty *et al*. 1982, Santantonio and Hermann 1985, Fairley and Alexander 1985). It is generally recognized that separating fine root biomass into the live and dead components greatly enhances the detection of seasonal dynamics and therefore improves the accuracy of production and mortality estimates.

A second approach to estimating fine root biomass production is based on ingrowth bags (Ericsson and Persson 1980, Coopersmith 1986). By introducing a root-free medium into the forest floor and mineral soil, the problem of simultaneous occcurance of production and mortality can be overcome. All live and dead fine roots encountered in the bag after the bag has been in the forest for a certain time period have been produced during that period. Although ingrowth bags solve some of the problems of the sequential coring method, the estimates of fine root biomass obtained from ingrowth bags may be biased by artefacts inherent in this method. Within a stand, fine root density in microsites increases with greater soil fertility, as discussed above. Introducing a disturbed, root-free medium into the soil may create a fertility gradient from the surrounding soil to the

ingrowth bag. If the fertitlity in the bag is greater than in the surrounding soil, fine root density will be higher in the bag and vice versa (cf. St. John 1983, Coopersmith 1986, Cuevas and Medina 1983 as discussed in Section 2.3). Furthermore, the effects of severing roots in the process of inserting the root ingrowth bag, on the subsequent growth of those roots has not been examined.

A third approach to measuring fine root dynamics involves observation windows or observation tubes. These are transparent plates or tubes which are placed in the forest floor and mineral soil. They permit regular monitoring of the same population of fine roots over a period of time. A number of artefacts are introduced by such observation devices, however (Bohm 1979). They are generally not suitable for a quantitative estimate of fine root production but are a valuable tool in the determination of fine root growth rhythms.

Nadelhoffer *et al.* (1985) used a nitrogen budget approach to determine fine root production and turnover. They established nitrogen budgets for several forest ecosystems and estimated fine root production by assuming that mineralized N not accounted for by plant uptake and allocation to aboveground litterfall and perennial tissues had been taken up by vegetation and allocated to fine roots. By knowing the concentration of N in the fine roots this is

claimed to permit an estimate of fine root production and turnover.

The development of an annual nutrient budget at an ecosystem level is a complex task which involves many assumptions concerning the unaccounted-for portion of the nitrogen budget (cf. Martin 1985 concerning denitrification). One assumption made by Nadelhoffer *et al.* (1985) was that "nitrogen use efficiency" (i.e. the amount of N required to produce one unit of N in fine root biomass) was the same for all species and levels of nitrogen availability. It is difficult to accept this assumption in the absence of any consideration of internal redistribution of N in above- and belowground biomass components. Many other processes have to be understood and measured in more detail before an ecosystem level N-budget can become a reliable method of estimating fine root production and turnover.

From this review one can conclude that estimating fine root production from direct measurements of the seasonal dynamics of fine root biomass is, in spite of its shortcomings, the most reliable of the currently availables approach in ecosystems where a strong seasonal amplitude in live and dead fine root biomass can be expected.

3. METHODS

3.1 Location and description of the study sites

The five study sites are located in research installations of the Forest Productivity Committee, British Columbia Ministry of Forests and Lands, on Vancouver Island. The selected installations contain up to 18 plots, including two untreated control plots.

The installations selected for this study are on the east side of Vancouver Island in the rain shadow of the Vancouver Island Mountains. Table 3.1 gives the location, installation number and plot number of each of the five study sites, which are referred to as stands A through E. Site index (m at breast-height age 50) (Bruce 1981) increased from A to E.

STAND	INSTAL-LATION	PLOT	LOCATION	LATITUDE/ LONGITUDE
A	71	14	Campbell River	50°02'/125°29'
B	2	6	Chemainus	48°50'/123°50'
C	5	10	Bowser	49°25'/124°48'
D	16	2	Campbell River	49°58'/125°30'
E	72	14	Cowichan Lake	48°49'/124°07'

Table 3.1 The designation of the five study sites assigned by the Forest Productivity Committee (Installation and Plot numbers), and their location.

Figure 3.1 shows the location of the installations. One control plot within each installation was selected for root sampling. Plots are square (22.36 m x 22.36 m) and have an area of 0.05 ha.

Figure 3.1 The location of the five study sites on Vancouver Island, British Columbia, Canada.

Table 3.2 classifies the stands according to the biogeoclimatic ecosystem classification system (Klinka *et al*. 1984, Krajina 1969), and presents mean annual precipitation and temperature data from nearby climatic recording stations (Environment Canada [1982]). Four installations are within the Wetter Maritime Coastal Douglas-fir (CDFb) subzone and one is in the Vancouver Island Drier Maritime Coastal Western Hemlock (CWHa1) variant (Table 3.1) (Klinka *et al*. 1984; Krajina 1969)

STAND	INSTAL-LATION	BEC	MEAN ANNUAL PRECIPITATION (mm)	MEAN ANNUAL TEMPERATURE (°C)
A	71	CDFb	1406[1]	8.2
B	2	CDFb	1103[2]	9.3
C	5	CDFb	1714[3]	9.3
D	16	CDFb	1406[1]	8.2
E	72	CWHa1	2122[4]	9.1

Climatic Data from Environment Canada [1982] for

1 Cambell River Airport
2 Nanaimo Airport
3 Mud Bay Fisheries
4 Cowichan Lake Research Station

Table 3.2 Biogeoclimatic ecosystem classification (BEC), mean annual precipitation and mean annual temperature for the five study sites.

Table 3.3 lists selected environmental characteristics.

Stand characteristics are summarized in Table 3.4.

STAND	ELEVATION (m)	PARENT MATERIAL	SOIL CLASSIFICATION	DRAINAGE
A	244	morainal blanket	Eluviated Dystric Brunisol	well drained
B	419	morainal blanket	Eluviated Dystric Brunisol	moderately well drained
C	360	fluvial	Duric Humoferric Podzol	well drained
D	335	morainal blanket	Duric Humoferric Podzol	moderately well drained
E	229	morainal blanket	Duric Humoferric Podzol	moderately well drained

Table 3.3 Selected environmental characteristics of the five study sites. Data from Smith 1979.

STAND	INSTAL-LATION	SITE INDEX (m@50)	AGE (years)	BA/ha (m^2/ha)	BA/ha %D.F.	STEMS/ha (No.)	STEMS/ha %D.F.
A	71	25	42	43.5	98	2420	97
B	2	31	43	49.9	67	2960	40
C	5	33	40	45.3	97	1420	87
D	16	34	33	39.1	98	2000	98
E	72	41	71	73.3	96	460	96

Table 3.4 Selected stand characteristics of the five study sites. %D.F.

Figure 3.2 Photograph of Stand A (Installation 71, Plot 14) near Campbell River, Vancouver Island.

Figure 3.3 Photograph of Stand B (Installation 2, Plot 6) near Chemainus, Vancouver Island.

Figure 3.4 Photograph of Stand C (Installation 5, Plot 10) near Bowser, Vancouver Island.

Figure 3.5 Photograph of Stand D (Installation 16, Plot 2) near Campbell River, Vancouver Island.

Figure 3.6 Photograph of Stand E (Installation 72, Plot 14) near Cowichan Lake, Vancouver Island.

In four of the five stands, Douglas-fir accounted for 96% or more of the overstory basal area (Table 3.4). In Stands A and C, western hemlock (*Tsuga heterophylla* (Ralf.) Sarg.) accounted for 1.5% and 3% of the basal area, respectively. Two percent of the basal area in Stand D was western redcedar (*Thuja plicata* Donn), and Stand E contained one bigleaf maple (*Acer macrophyllum* Pursh.) which contributed 3.8% of the basal area in that plot. In contrast, while the upper canopy layer of Stand B was predominantly Douglas-fir, there was a well-developed lower canopy layer of western hemlock which accounted for 32% of the basal area; sacttered western redcedar contributed 1% of the basal area.

A list of shrubs, herbs and mosses for each stand is presented in Appendix 6.

The understory vegetation of Stand A (Figure 3.2) was in some parts dominated by *Gaultheria shallon* Pursh, while other parts were dominated by a dense moss cover of *Kindbergia oregana* (Sull.) Ochyra and *Hylocomium splendens* (Hedw.) B.S.G. There were scattered individuals of *Mahonia nervosa* (Pursh) Nutt. and some patches of *Pteridium aquilinum* (L.) Kuhn.

Stand B (Figure 3.3) had the highest cover value (40%) of salal and the lowest species diversity all five stands. *Kindbergia oregana* and *Hylocomium splendens* were the predominant mosses, and there was some *Mahonia nervosa*.

Stand C (Figure 3.4) had a low stand density and a relatively well illuminated forest floor covered by a thick layer of mosses dominated by *Kindbergia oregana*, *Hylocomium splendens*, *Rhytidiadelphus loreus* (Hedw.) Warnst., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., and *Rhytidiopsis robusta* (Hook.) Broth. In spite of the higher light levels, the % cover of shrubs (salal, *Mahonia nervosa*, *Rubus* spp.) and herbs (*Achlys triphylla* (Sm.) DC., *Polystichum munitum* (Kaufl.) Presl, *Pteridium aquilinum*) was low.

The shrub layer of Stand D (Figure 3.5) had less than 5% cover and consisted of salal, *Mahonia nervosa*, and *Symphori-carpus albus* (L.) Blake. The main herbs were *Achlys*

triphylla, *Mycelis muralis* (L.) Dumort., and some *Polystichum munitum*.

The understory vegetation of Stand E was dominated by *Polystichum munitum* and *Achlys triphylla*. Other herbs frequently encountered were *Tiarella laciniata* Hook., *Tiarella trifoliata* L., and *Trientalis latifolia* Hook. Mosses (*Kindbergia oregana*, *Hylocomium splendens*) were mostly confinded to logs and rocks.

3.2 Sample Collection

The selection of sampling dates was based on Vogt *et al*. (1986) who recommended coordinating fine root sampling with the phenological activities of the trees. The first and last sampling dates were chosen to be just prior to bud break, at which time the largest amount of live fine roots can be expected (cf. Kramer and Kozlowski 1979). Six additional sampling dates throughout the remainder of the year were choosen, but because of financial and time costraints only five sets of samples were processed for all sites. The samples from one site for one additional date were processed. Table 3.5 lists sampling dates, the intervals in weeks between those dates, and the number of cores which were processed. Laboratory processing required over 24 hours per core, which was slower than anticipated and not all samples could be sorted.

DATES	INTERVAL (weeks)	PROCESSED	CORES PER STAND
May 13 - 18, 1985		5 stands	17
June 24 - 29, 1985	6	5 stands	10
Aug 10 - 14, 1985	7	5 stands	10
Oct 3 - 6, 1985	8	5 stands	10
Feb 3 - 6, 1986	18	1 stand	10
May 12 - 16, 1986	14	5 stands	10

Table 3.5 The sampling dates and the number of cores per stand processed for each of those dates.

Sample locations within each plot were randomly located using an x-y grid. Rocks, which occurred frequently in some of the plots, occasionally clogged up the soil corer or prevented its penetration of the soil. If it was physically impossible to obtain a sample at the selected position, an adjacent spot was chosen at random.

Soil cores were obtained with a schedule 40 steel pipe, (5.25 cm inside wall diameter, 4 mm wall thickness, 90 cm long), which had a reinforcement welded to the top (Figure 3.7). A four pound sledge hammer was used to drive the pipe into the soil. After reaching a depth of 30 cm, the corer was removed from the soil and the sample was emptied into a plastic bin. Mineral soil and forest floor sections of the sample were separated and packaged in labelled plastic bags.

The pipe was then re-inserted into the hole to remove a sample from the 30 to 50 cm soil depth.

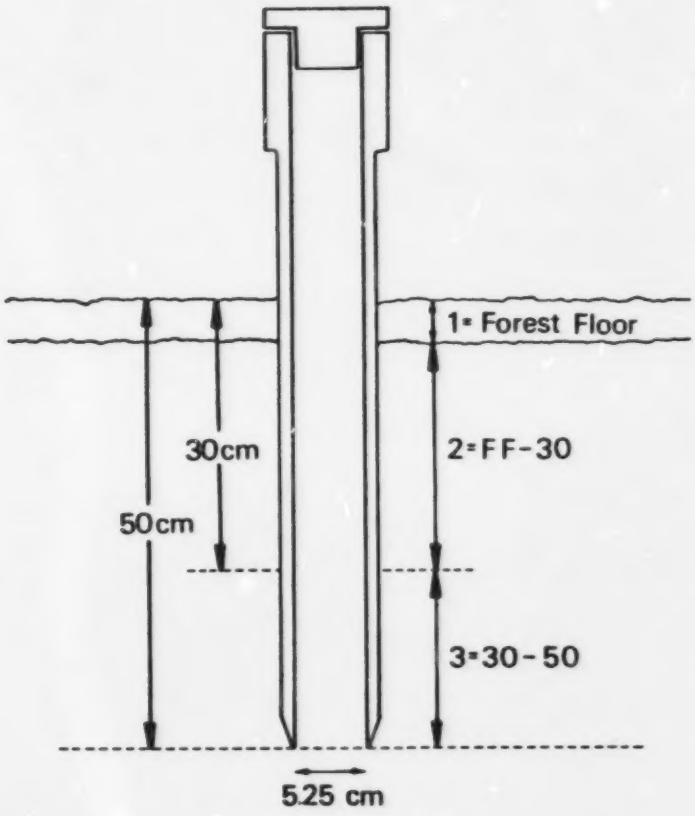

Figure 3.7 Schematic diagram of the soil corer and the sampling depths collected with it.

During field sampling, samples were kept in cold storage whenever possible. After returning to Vancouver samples were placed in cold storage at 2°C until processed. Samples were not frozen because this would have increased the difficulties in distinguishing live from dead fine roots during processing (K. Vogt, pers. comm.).

Figure 3.8 Photograph of the soil corer in the field. The corer has been driven into the soil to a depth of 30 cm.

3.3 Sample Preparation

In the laboratory, samples were carefully rinsed with tap water over two nested sieves, the upper one with a 2 mm

and the lower one with a 0.5 mm mesh size. After most fine sand and clay particles had been washed through the sieves, organic materials were separated from the remaining coarse mineral material by carefully pouring off the water with the organic material. The organic material in the 2 mm sieve then was processed according to the criteria described below. The fine organic material from the 0.5 mm sieve consisted of plant particles in various stages of decomposition, charcoal particles, and some fine root tips. Further processing of this material required the use of a dissecting microscope. The origin of most organic fragments could not be identified and processing was prohibitively time consuming. After initial trials it was decided not to sort this material, and the organic material in the 0.5 mm sieve was thereafter simply dried and weighed. Dry weight and ash content data for this component are listed as category R (residual) in the Appendix.

3.4 Decision criteria for the sorting of roots

Fine and coarse roots and other organic material in the 2 mm mesh size sieve were hand sorted into 12 classes as outlined below. Non-root material, such as twigs, salal leaves, etc., was discarded. During processing the root material was continuously immersed in water. Classified root

segments were transfered into labelled plastic petri dishes containing deionized water.

At the outset of the study, roots were collected from a variety of species present on the study sites. A set of reference samples was established to assist in the subsequent identification of species.

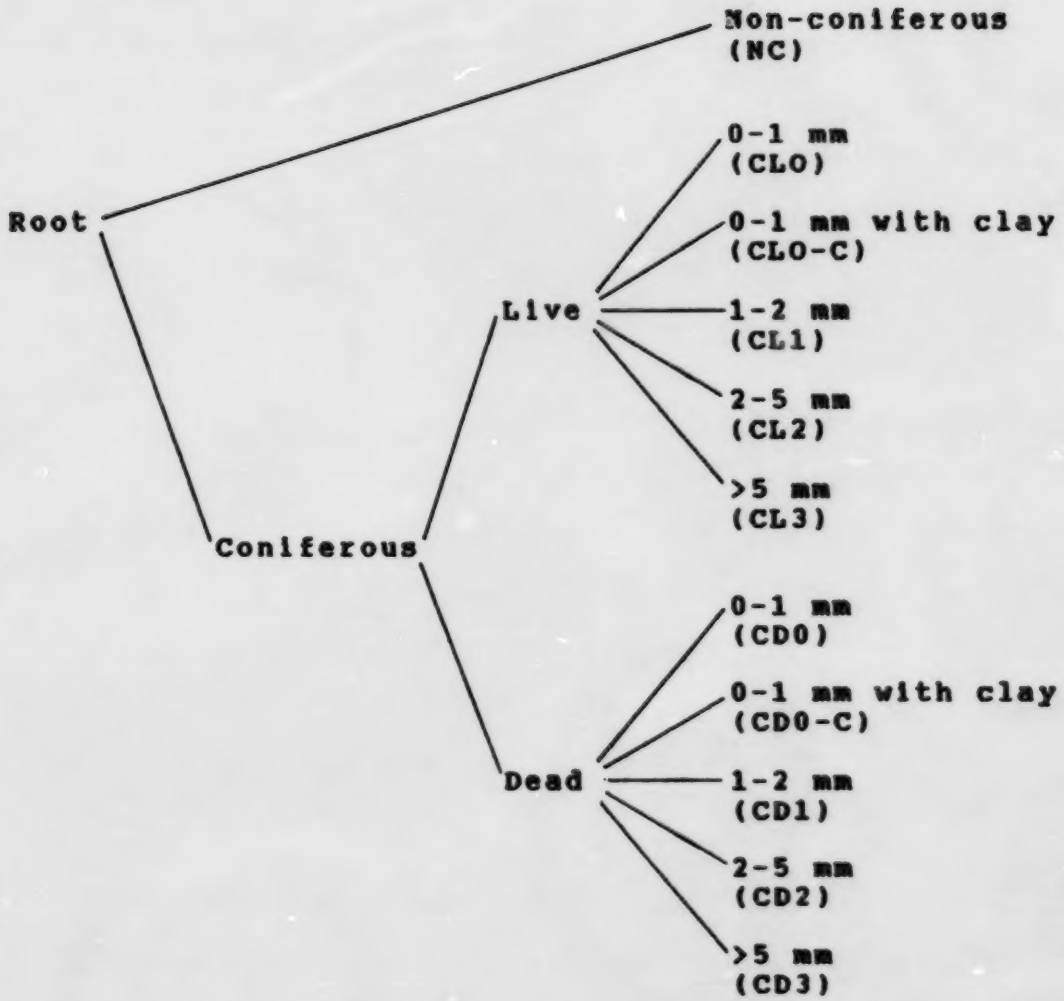

Figure 3.9 Schematic presentation of the classification of roots into 11 categories as used in this study.

Figure 3.9 shows a diagram of the 11 classes into which roots were separated during processing. Mycorrhizal hyphae and other fungal materials were classified in a separate category (M).

Both live and dead coniferous roots were classified into four diameter classes (0-1 mm, 1-2 mm, 2-5 mm, and > 5mm). The 0-1 mm diameter class of both live and dead roots was further subdivided into fine roots with clay particles adhering to the surface (CL0-C and CD0-C, respectively) and those without. Soil particles embedded in the mycorrhizal mantle and in mycorrhizal clusters could not be removed.

Non-coniferous roots (NC) were not separated into subclasses. The very small diameter of the roots of many herbaceous and shrub species did not permit classification into live and dead roots. In retrospect, between sample variation would have been reduced by separating the large rhizomes of ferns (*Polystichum munitum, Pteridium aquilinum)*, which were found in some samples, from other non-coniferous roots.

The most difficult and time consuming task was the differentiation between live and dead coniferous fine roots. We employed criteria from the literature (Santantonio and Hermann 1985, Persson 1983), from personal communications with other researchers, and from our own observations. These criteria included colour, texture and tensile strength of the roots. When in doubt, iodine stain was used to test for

the presence of starch granules. If starch was present roots were classified as living at the time of sampling. Details of the criteria are as follows.

COLOUR: The periderm of live coniferous roots is almost black, sometimes with some red. The secondary xylem is off-white. In contrast, the surface colour of dead roots is greyish. The secondary xylem is brownish to yellowish.

TEXTURE: Dead roots are brittle with a low tensile strength. Tensile strength is assessed subjectively and varies with root diameter. Pulling a live fine root apart using stainless steel tweezers causes a "snapping" sound which is much less audible in dead roots. The secondary phloem of dead roots separates readily from the secondary xylem and the root often shows a "distinct girdled pattern" of separated bark segments along the central cylinder. Dead roots often feel soggy or mushy and are not pliable.

FLOTATION: A root segment which floats on the surface is most likely dead. Only some of the dead roots float, however.

We placed great emphasis on a consistent application of the sorting criteria. Samples were often cross-checked by an experienced technician. New staff were carefully trained and their work was closely monitored and re-examined. After some training, very consistent results were obtained by all technicians.

Processing times varied greatly depending on the characteristics of the samples. Forest floor samples, although of much smaller volume, tended to require more time than mineral soil samples. An average of approximately 8 hours per sample or about 24 hours per core was required for sorting. Additional time was required for drying, weighing and, for a subset of samples, ash content determination.

When the processing of a sample was completed, the water was drained from the petri dishes and the roots were dried in a forced air oven at 70°C for 48 hours. Root samples were weighed to the nearest .001 gram. A total of 986 samples were processed, including the drying and weighing of about 8000 petri dishes with classified root material. All dried samples were retained for further nutrient analysis.

3.5 Ash content

Soil particles adhering to the surface of roots after careful rinsing and washing cannot be removed without loss of organic substance from the fine roots. If soil particles are included in the dry weights of roots, an overestimate of fine root biomass can occur. This error, which can be serious in fine textured soils, should be corrected by obtaining ash-free dry weights. Ovendry samples (redried at

70°C for 24 hours) were weighed into porcelain crucibles and heated to 470°C for 4 hours. Ash content was expressed as a percentage of ovendry weight.

3.6 Data processing and analyses

The extent and complexity of the data sets required the development of several computer programs to facilitate data processing. The two main data sets contain the data on ash-contents of fine root samples and on fine root dry weights. For the calculation of ash-free dry weights these two data sets had to be combined.

A computer program was developed for the conversion of root dry weights to ash-free dry weights. This program verified, for each of the approximately 8000 samples whether or not the actual ash content was known. If this was the case, the sample's actual ash content was used for the conversion to an ash-free dry weight. If the actual ash content of a sample was unknown, the mean ash content for that sample's installation, horizon, and root class was used for the conversion. If this mean was based on less than 3 observations, the mean of the sample's root class and horizon basede on all five installations was used.

The ash-free weights of the CL0 and CL0-C and the CD0 and CD0-C root classes were then added to obtain the ash-

free dry weights of the live and dead roots in the 0-1 mm diameter classes. Two additional classes were introduced at this point: they represent the live and dead fine roots in the 0-2 mm diameter classes (0-1 mm plus 1-2 mm). Root samples originated from three different soil layers: forest floor (1), 0-30 cm mineral soil (2), and 30-50 cm mineral soil (3). Three additional horizons were introduced to permit the computation of standard deviations and standard errors. These were forest floor plus the upper mineral soil layer (4=1+2), the sum of the two mineral soil layers (5=2+3), and the sum of all three horizons (6=1+2+3).

The computer program then calculated, for each of the 2700 sampling strata (5 Installations x 6 sampling dates x 6 horizons x 15 root classes), the mean, standard deviation and standard error of the ash-free root dry weights and the number of cores collected. These parameters were then tabulated and printed to an output file. An example of such a file is shown in Appendix 3. This information was also printed to a second output file which subsequently serves as the input data file for the computation of fine root production and mortality.

3.7 Calculation of production and mortality estimates

An interactive computer program has been developed for the calculation of fine root production and mortality estimates. It applies three different computational methods

to the data which describe the seasonal dynamics of live and dead fine root biomass. The three methods are based on (1) the decision matrix (Fairley and Alexander 1985, McClaugherty *et al*. 1982), (2) all changes in live fine root biomass, and (3) significant changes in live fine root biomass.

DECISION MATRIX: The decision matrix (DM) presents a series of equations which calculate fine root production, mortality, and disappearance based on the observed changes in both live and dead fine root biomass. The decision as to which set of equations to apply for a given sampling interval is based on a matrix which describes all possible combinations of increases and decreases in live and dead fine root biomass (Figure 3.10). For example, if live fine root biomass increases and dead biomass decreases, the set of equations to use is in the lower left of the decision matrix.

LIVE

DEAD	increase	decrease	
		$\Delta B^{dead} > \Delta B^{live}$	$\Delta B^{live} > \Delta B^{dead}$
increase	$P = \Delta B^{live} + \Delta B^{dead}$ $M = \Delta B^{dead}$ $D = 0$	$P = \Delta B^{live} + \Delta B^{dead}$ $M = \Delta B^{dead}$ $D = 0$	$P = 0$ $M = -\Delta B^{live}$ $D = -\Delta B^{live} - \Delta B^{dead}$
decrease	$P = \Delta B^{live}$ $M = 0$ $D = -\Delta B^{dead}$	$P = 0$ $M = -\Delta B^{live}$ $D = -\Delta B^{live} - \Delta B^{dead}$	

Decision matrix illustrating the equations used for estimating fine root production, mortality and fine dead root disappearance. The appropriate quadrant is chosen according to the direction of change in the live and dead standing biomasses (B) during the interval between two sampling dates. Production (P), mortality (M) and disappearance (D) are calculated using the equations in the indicated quadrants. In the top right quadrant a choice of equations is given depending on whether the observed change is larger in the dead or in the live biomass. Derivation of the equations are discussed in the text. Annual estimates are calculated by summing the estimates from all sampling intervals within the year.

Figure 3.10 The decision matrix as presented by Fairley and Alexander (1985).

The computer program calculates the changes in live and dead fine root biomass between sampling dates and applies the appropriate set of equations for the computation of production and mortality estimates. The annual total is based on the sum of the estimates obtained for each sampling interval.

ALL CHANGES: The second method (AC) is solely based on the observed changes in the live fine root biomass. All increases in live fine root biomass from one sampling date to the next are considered to be the sole result of production, and all decreases are considered to be the sole

result of mortality. The sum of the estimates for all sampling periods constitutes the annual totals.

SIGNIFICANT CHANGES: The third method (SC) is again solely based on the observed changes in live fine root biomass but in this method only significant changes in fine root biomass are attributed to production or mortality. The student t-test (Zar 1984) is applied at $p \leq .05$ to successive means of live fine root biomass to test for statistical differences. If the means at t_i and t_{i+1} are not significantly different, the program establishes the direction of change between the two means. If the trend is continued from the mean at t_{i+1} to the mean at t_{i+2} then the means at t_i and t_{i+2} are tested for significant differences. If the trend reverses, the means at t_{i+1} and t_{i+2} are tested for significant difference. When two sample means are compared, the program first tests whether or not the two variances associated with the means are equal. If yes, the student t-test is applied. If the variances are unequal, Welch's approximate t-test is applied (Zar 1984:131). The sum of all significant increases represents annual production and the sum of all significant decreases represents annual mortality.

The computer program was used to calculate fine root production and mortality for each of five root classes (0-2 mm, 0-1 mm, 1-2 mm, 2-5 mm, >5 mm) and for each of six horizons (see above) according to the above three methods.

For the SC-method the program will perform the computations at any user defined probability level. An example of the output file is presented in Appendix 4. The program also calculates a number of statistics which facilitate the comparison of the different computational methods. Appendix 5 contains an example of such comparisons, which will be discussed in detail in Section 4.4.1 of this report.

3.8 Nitrogen mineralization rates

In August 1986, 10 randomly located samples of forest floor and mineral soil were collected from each of the five plots. Two samples, one of at least 10 cm x 10 cm of forest floor and one of mineral soil to a depth of 20 cm, were collected at each sampling location. Distinct forest floor layers were poorly developed or absent, and no attempt was made to separate them. All living aboveground plant material (herbs, mosses) was removed.

All samples were air dried at room temperature. Mineral soil samples were passed through a 2 mm mesh sieve and the coarse fragments discarded. Forest floor material was gently grated through a 2 mm sieve. Three $\pm$ 0.1 grams of forest floor material and 5.0 $\pm$ 0.1 grams of mineral soil were weighed into separate test tubes and approximately 25 ml and 28 ml of deionized water were added, respectively. Samples were thoroughly mixed using a Vortex mixer. The thread of the test tubes was covered with teflon tape and the tubes

sealed with screw caps. Blanks, containing deionized water only, were also included in the incubations. Two of the ten samples per plot were incubated in triplicate.

Samples were incubated at 40°C for seven days. After incubation, samples were hand shaken and filtered through Whatman No. 41 filter paper. Test tubes and filters were rinsed with aproximately 70 ml of 2N KCl. The sample was then brought to a total volume of 100 ml with 2N KCl and transferred into labelled plastic bottles which were stored at 2 °C. Within one to five days, samples were analysed for NH_4^+ content using a Technicon Autoanalyzer. Results are reported in mg NH_4^+ per 100 g substrate. No correction for pre-incubation ammonium levels was applied (Powers 1980).

4. RESULTS AND DISCUSSION

4.1 Nitrogen Mineralization rates

Nitrogen mineralization rates (N_{min}) as determined by anaerobic incubation varied greatly between plots, for both mineral soil and forest floor samples. Table 4.1 presents means and standard deviations for N_{min}. Mineralization rates in the mineral soil ranged from 17.0 ppm to 75.8 ppm for the stands with the lowest (Stand A) and highest (Stand E) site index, respectively. The mineralization rates in the forest floor were up to an order of magnitude higher and ranged from 281.7 to 594.6 ppm for sites D and E, respectively.

STAND	INSTAL LATION	SITE INDEX (m@50)	MINERAL SOIL (ppm)	FOREST FLOOR (ppm)
A	71	25	17.0 a (5.4)	303.2 a (72.9)
B	2	31	24.8 a (12.3)	294.5 a (112.7)
C	5	33	58.6 b,c (40.7)	368.2 a (48.8)
D	16	34	30.5 a,c (16.3)	281.7 a (118.1)
E	72	41	75.8 d (35.4)	594.6 b (78.2)

Table 4.1 Nitrogen mineralization indices obtained through anaerobic incubation. Mean (standard deviation) of 10 samples per plot (except site C, forest floor n=8). Samples within a column followed by the same letter are not significantly different ($p \leq .05$).

4.2 Ash content of root samples

The ash content of 2225 root samples in 195 strata (5 study sites x 3 horizons x 13 root classes) was determined as part of this study. Ash contents varied between horizons, between root diameter classes, between live and dead roots of the same diameter class, and between study sites.

Root Class	Horizon		
	Forest floor	FF-30 cm	30-50 cm
CL0 0-1 mm	10.30 (0.58) n=104	14.49 (0.50) n=113	17.11 (0.79) n= 94
CL0-C 0-1 mm	44.39 (2.55) n= 35	44.74 (1.20) n= 96	43.56 (1.65) n= 63
CL1 1-2 mm	6.45 (0.72) n= 47	9.83 (0.55) n= 91	12.66 (0.75) n= 61
CD0 0-1 mm	15.92 (0.86) n= 82	21.16 (0.78) n=101	22.07 (0.88) n= 92
CD0-C 0-1 mm	49.31 (3.07) n= 20	53.54 (1.44) n= 73	53.29 (1.70) n= 47
CD1 1-2 mm	5.61 (1.21) n= 6	14.22 (1.23) n= 39	17.17 (1.37) n= 33

Table 4.2 Mean, (standard error) and sample size (n) for the ash content expressed in percent of sample dry weight for the three horizons and for six root classes. Data are mean values for the five study sites. Appendix 2 contains full details for 195 strata (5 study sites x 3 horizons x 13 root classes).

Table 4.2 presents means for the combined data from the five study sites for 6 root classes and 3 horizons. Ash

contents increased with depth in the soil and tended to be higher for dead than for live roots in the same diameter class.

The roots in the 0-1 mm diameter class were divided into two categories: with and without "clay" particles (probably a mixture of silt and clay-sized particles) adhering to the mycorrhizal clusters (see Section 3.4). Although only a small portion of the fine roots of most samples was classified as "with clay" (CL0-C, CD0-C), the data in Table 4.2 emphasize the need for this extra category. The "with clay" classes had two to four times higher ash contents than the "without clay" classes. Failing to separate these two additional classes would have introduced considerable bias and increased the variability in the estimates of ash-free fine root dry weights.

4.3 Fine Root Biomass

4.3.1 Fine root biomass in May 1985

Live and dead fine root biomass are dynamic and show a distinct seasonal pattern which will be described in the next section. The static comparison of live fine root biomass at the five study sites presented in this section is based on the values obtained in May 1985. Note that in some cases these values differ significantly from the values in May 1986; this will be discussed later.

The total mean live root biomass and the biomass in each of the three soil layers in May 1985 is shown in Table 4.1. Forest floor thickness (FFT) based on 20 measurements per plot is shown in the same Table. Fine root biomass in the forest floor ranged from 23.6 g/m^2 in Stand E to 212.3 g/m^2 in Stand B, a nine-fold difference. The mineral soil layer to a depth of 30 cm (measured from the upper surface of the forest floor) contained the highest amount of fine roots, ranging from 109.9 to 436.6 g/m^2. The 30 to 50 cm mineral soil layer contained from 48.5 to 142.5 g/m^2 fine roots. Total fine root biomass ranged from 182 g/m^2 in Stand E to 791g/m^2 in Stand B, more than a four-fold difference.

STAND	SI (m@50)	FFT (mm)	LIVE FINE ROOT BIOMASS (g/m^2)				
			FF	0-30 cm	30-50 cm	FF-50 cm	n
A	25	18.1 (1.0)	63.4 (16.7)	243.5 (49.1)	98.0 (23.9)	404.9 (80.7)	15
B	31	19.2 (2.5)	212.3 (24.8)	436.6 (44.1)	142.5 (23.2)	791.5 (56.2)	17
C	33	13.9 (1.3)	87.6 (24.8)	160.3 (24.5)	63.2 (12.8)	311.2 (43.3)	16
D	35	13.3 (1.2)	97.6 (17.5)	228.1 (31.2)	106.7 (20.0)	432.5 (42.5)	17
E	41	12.2 (1.1)	23.6 (11.7)	109.9 (12.8)	48.5 (14.9)	182.0 (17.6)	17

Table 4.3 Mean, (standard error) and sample size (n) of live fine (0-2 mm) root biomass in May 1985 at the five study sites. Mean and standard error of forest floor thickness (FFT) are based on 20 measurements taken in each stand. SI refers to the Site Index in meters at breast-height age 50.

The distribution of live fine roots among the 3 soil layers was approximately 1:2:1 for the forest floor : 0-30 cm : 30-50 cm layers (Table 4.4). Thirteen to 28% of all live fine roots to a depth of 50 cm were found in the forest floor. About 51% to 60% were present in the 0-30 cm mineral soil layer, and 20% to 27% were in the 30-50 cm soil layer. Note, however, that the mean forest floor thickness was less than 2 cm in all five study sites.

STAND	SI (m@50)	FFT (mm)	LIVE FINE ROOT BIOMASS (% of total)			
			FF	0-30 cm	30-50 cm	FF-50 cm
A	25	18.1	15.7	60.1	24.2	100.0
B	31	19.2	26.8	55.2	18.0	100.0
C	33	13.9	28.1	51.5	20.3	100.0
D	35	13.3	22.6	52.7	24.7	100.0
E	41	12.2	13.0	60.4	26.6	100.0

Table 4.4 Live fine root biomass in each layer, expressed as percentage of the total fine root biomass, in May 1985 for each of the five stands.

The importance of the upper soil layer and the forest floor becomes even clearer when fine root biomass is expressed on a per volume (g/m^3)rather than on a per area (g/m^2) basis (Table 4.5). Live fine root biomass (g/m^3) decreased from 11057 g/m^3 in the forest floor to 713 g/m^3 in the 30-50 cm layer in Stand B. In Stand E, the live fine root biomass ranged from 1934 g/m^3 in the forest floor to 243 g/m^3 in the 30-50 cm mineral soil layer.

STAND	SI (m@50)	FFT (mm)	LIVE FINE ROOT BIOMASS (g/m^3)			
			FF	0-30 cm	30-50 cm	FF-50 cm
A	25	18.1	3503	864	490	810
B	31	19.2	11057	1555	713	1583
C	33	13.9	6302	560	316	622
D	35	13.3	7338	796	534	865
E	41	12.2	1934	382	243	364

Table 4.5 Live fine root biomass in May 1985 expressed on a volume basis (g/m^3) for three horizons and for the total soil layer to a depth of 50 cm for each of the five study sites.

Within each stand, nitrogen mineralization (as measured by anaerobic incubation) was higher in the forest floor than in the mineral soil, as was fine root density. Within each substrate, however, fine root density tended to decrease with increasing nitrogen mineralization rates, as shown in Figure 4.1 for mineral soil and in Figure 4.2 for forest floor. This decrease in fine root density was not significant ($r=-.732$, $p=.160$ for MS and $r=-.673$, $p=.213$ for FF) if all five stands were considered. Stand B, the stand which contains some western hemlock and western redcedar in addition to the Douglas-fir, had almost twice the fine root density in the 0-30 cm mineral soil layer compared to the remaining four stands. Excluding Stand B from the analysis, the relationship between fine root density and N_{min} (as shown by the lines in Figures 4.1 and 4.2) becomes highly

significant for the mineral soil (r=-.995, p=.005), but remains non-significant (r=-.731, p=.269) for the forest floor.

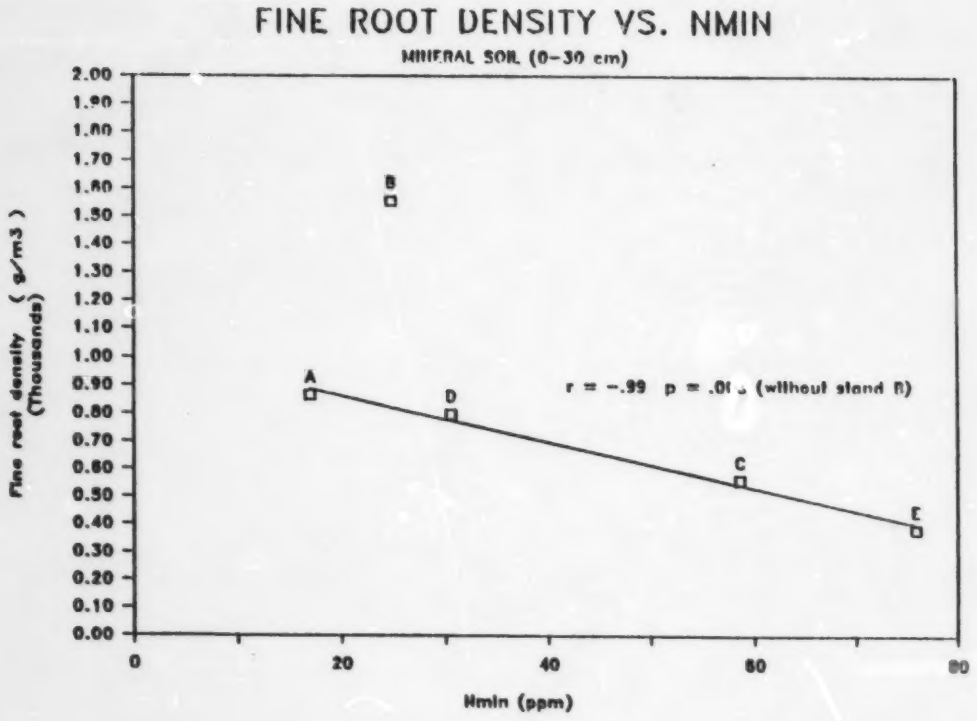

Figure 4.1 The relationship between fine root density and N_{min} in the mineral soil for the five stands. The line is based on four observations, excluding Stand B (r=-.995, p=.005).

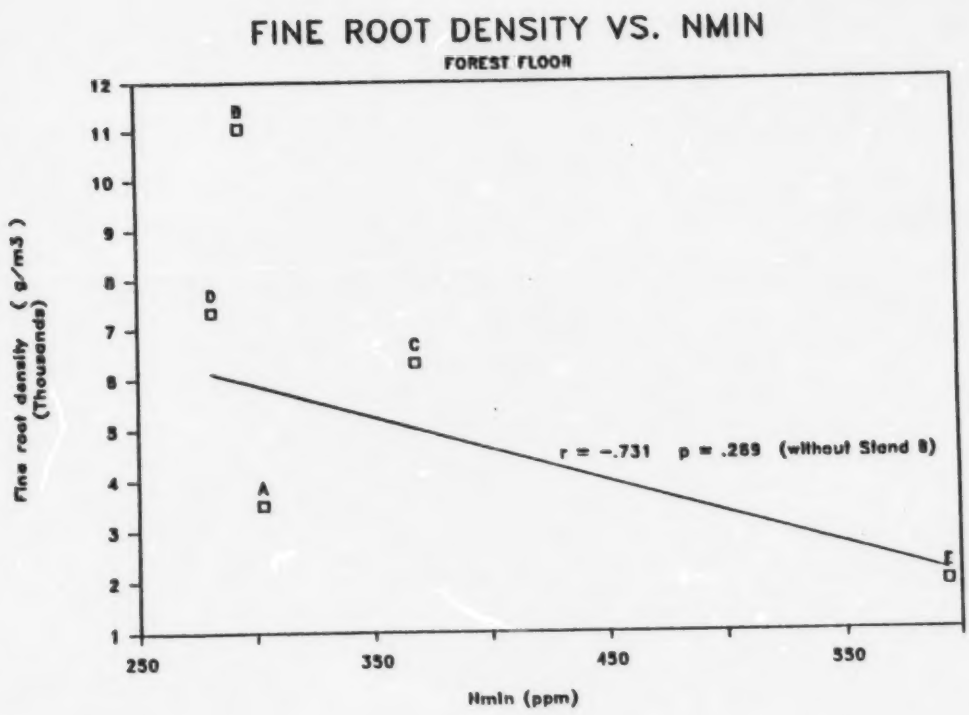

Figure 4.2 The relationship between fine root density and N_{min} in the forest floor for the five stands. The line is based on four observations, excluding Stand B (r=-.731, p=.269).

The relationships described in Figures 4.1 and 4.2 are only tentative because both fine root density and nitrogen mineralization rates are highly dynamic and vary over the course of the year. Furthermore, fine root density is based on the biomass estimates for May 1985 while N_{min} was determined for samples collected in August 1986.

4.3.2 Seasonal dynamics of root biomass

The seasonal dynamics of root biomass for live and dead fine (0-2 mm) and small (2-5 mm) roots and for non-coniferous roots are reported here. Roots greater than 5 mm in diameter were only occasionally present in the soil cores, and data on this root size class will not be presented. The mean ash-free dry weights, standard errors, and sample sizes for all root classes, all study sites and all sampling dates which were processed are listed in Appendix 3.

4.3.3 Seasonal dynamics of fine (0-2 mm) roots

The seasonal dynamics of live and dead fine (0-2 mm) root biomass of all five study sites is shown in Figure 4.3. Figure 4.4 displays live and dead fine root biomass with standard errors for each stand individually. Live fine root biomass shows a very similar trend in all 5 study sites. It peaked in the spring of 1985 and 1986 and was lowest at the early October or mid August sampling dates. From May to June (1985), live fine root biomass declined slightly in four study sites and increased slightly in Stand B. This was followed by a sharp decline at the August sampling date in all five stands. From August to early October, live fine biomass continued to decline in four stands and showed a

small increase in Stand E. From the low in the fall, biomass increased again to the May 1986 sampling date.

We were able to process the samples for one additional sampling date (early February) for Stand E. The resulting data point suggests that most of the increase in live fine root biomass occurred from February to May, i.e. during the spring rather than during the winter months.

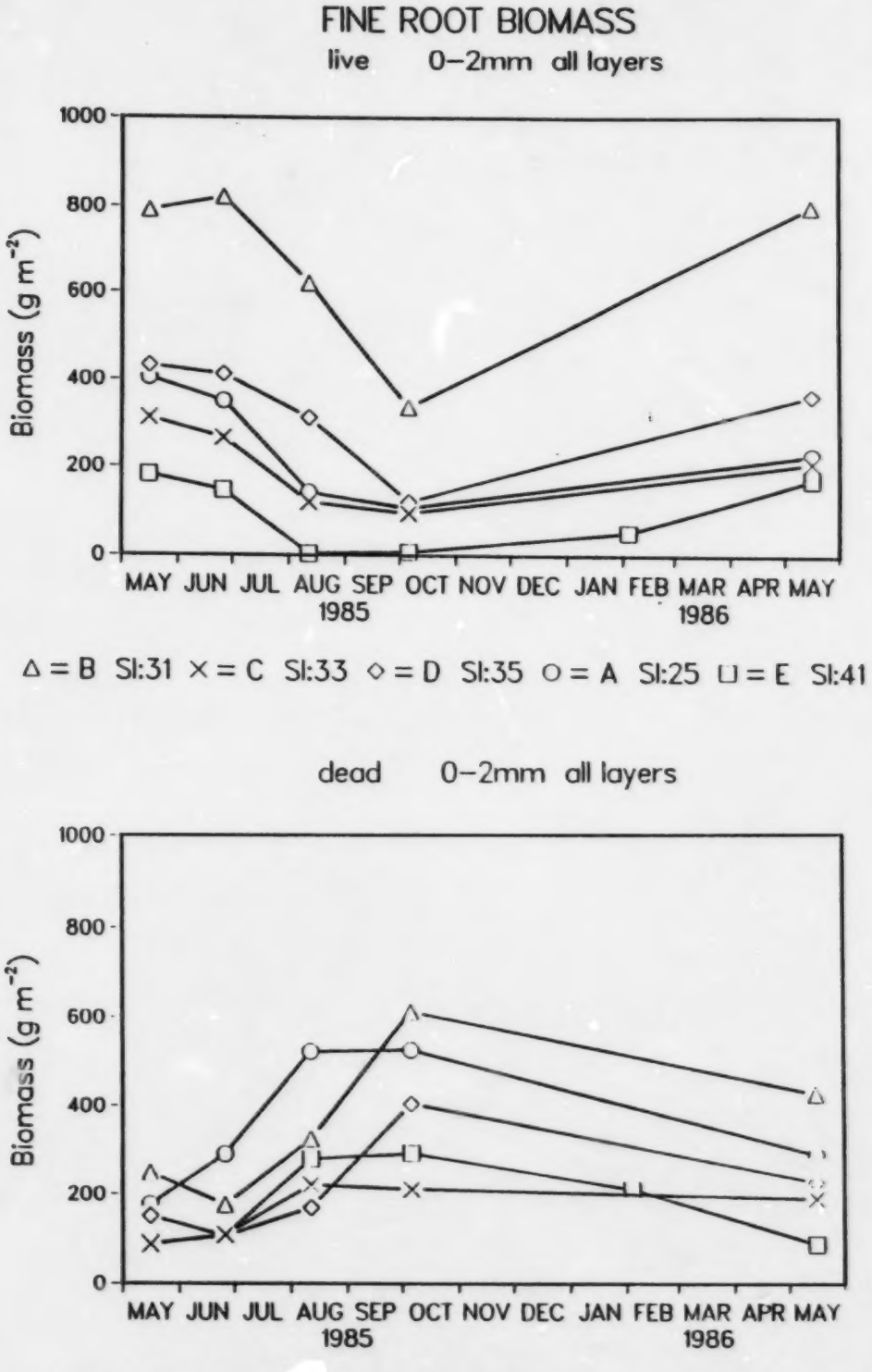
FINE ROOT BIOMASS
live 0–2mm all layers
Biomass (g m⁻²)
1000
800
600
400
200
0
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1985
1986
△ = B SI:31 × = C SI:33 ◇ = D SI:35 ○ = A SI:25 □ = E SI:41
dead 0–2mm all layers
Biomass (g m⁻²)
1000
800
600
400
200
0
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1985
1986
△ = B SI:31 × = C SI:33 ◇ = D SI:35 ○ = A SI:25 □ = E SI:41

Figure 4.3 Seasonal dynamics of live (top) and dead (bottom) fine root biomass in the 5 Stands. Data represent the mean of 10 samples per sampling date (15-17 for May 1985).

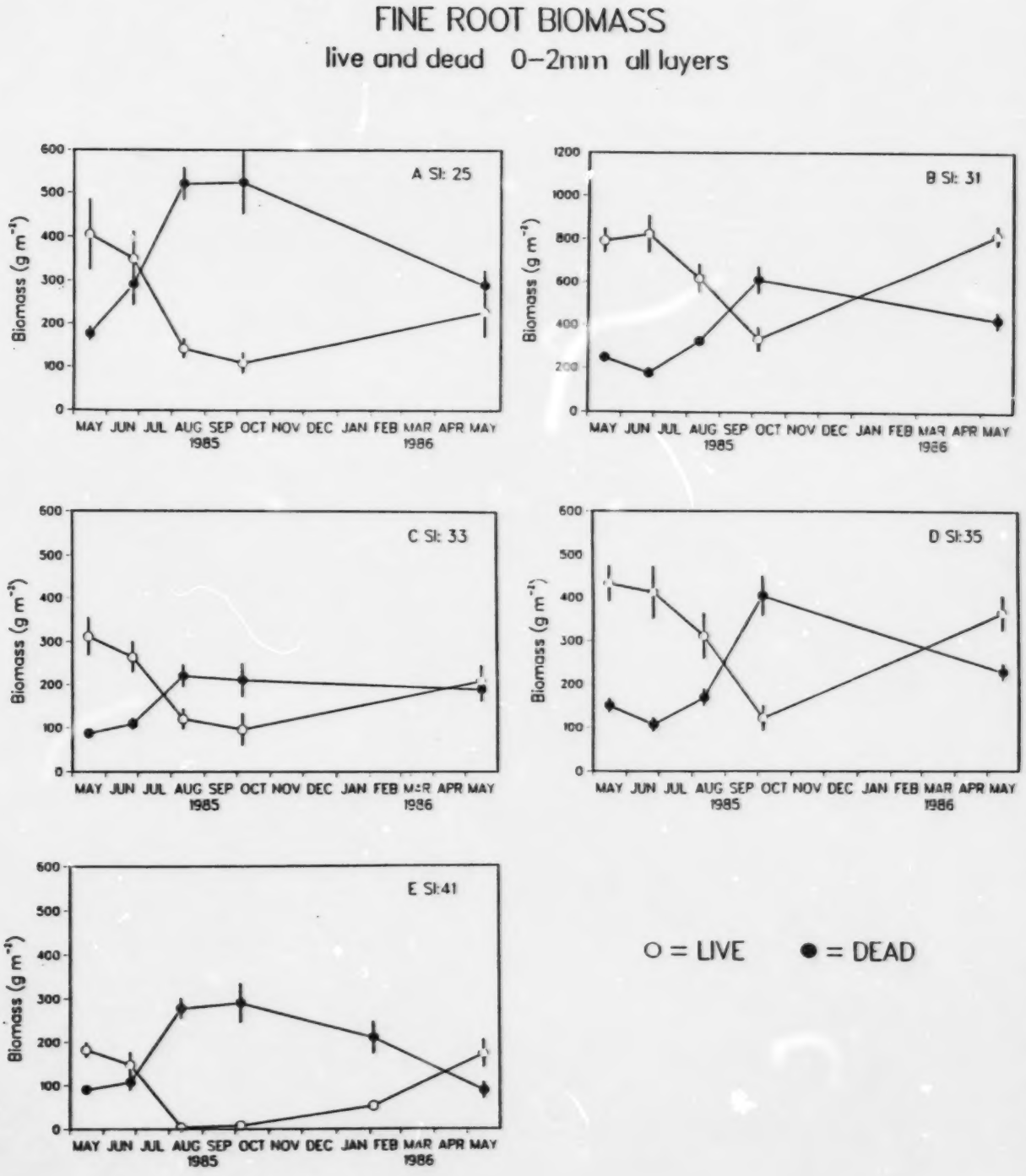

Figure 4.4 Seasonal dynamics of live and dead fine root biomass at each of the 5 Stands. Vertical bars represent ± 1 standard error.

Dead fine root biomass also showed similar trends in all five stands (Figures 4.3 and 4.4). Values increased in Stands A, C, and E but decreased in Stands B and D from mid May to the end of June. This was followed in all stands by a sharp increase to the August sampling date. For Stands A, C, and E, dead root biomass showed little change from August to October, but continued to increase during this period on Stands B and D. From October to May 1986 dead root biomass decreased in all five stands. The additional data point (February 1986) for Stand E suggests that disappearance was greater from February to May than during the winter months.

Live and dead fine root biomass dynamics displayed a very symetrical pattern (Figure 4.4). Most of the decreases in live fine root biomass were accompanied by increases in dead fine root biomass. When live fine root biomass increased, the dead biomass component decreased, presumably through decomposition.

Fine root mortality can be induced by moisture stress (Deans 1979). All five study sites experience a soil moisture deficit in a typical year. Figure 4.5 shows the 30 year average of mean monthly precipitation at Nanaimo Airport (Environment Canada [1982]) and the actual monthly precipitation for 1985 and the first six months of 1986 (Environment Canada pers. comm.). The summer of 1985 was unusually dry, with below average rainfall from May through August and no precipitation at all in July. Precipitation in

October 1985 was well above the 30 year average at Nanaimo Airport. This precipitation occurred, however, after the sampling date in the first week of October.

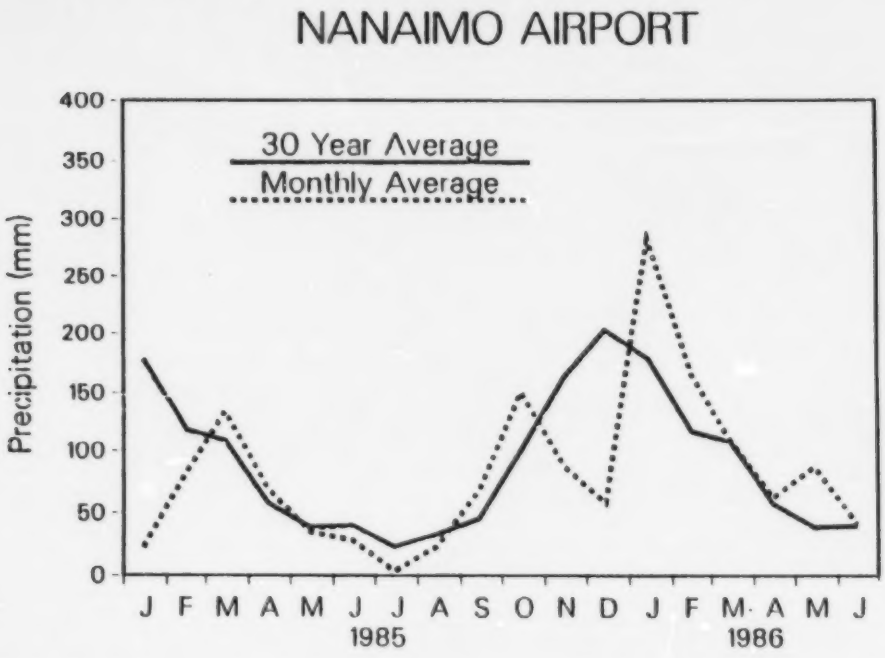

Figure 4.5 Mean monthly precipitation (30 year average) at Nanaimo Airport, and actual precipitation for 1985 and the first six months of 1986. (Environment Canada [1982] and pers. comm.)

Daily precipitation data were obtained from the Cowichan Lake Research Station, about 1 km from the location of Stand E. Figure 4.6 shows daily precipitation at the Research Station and live fine root biomass at Stand E. Only 16.8 mm of precipitation fell from June 24 to August 22, most of it on two consecutive days in early August. About 54 mm of precipitation occurred in early September, followed by another rain-free period of 21 days prior to the October sampling date.

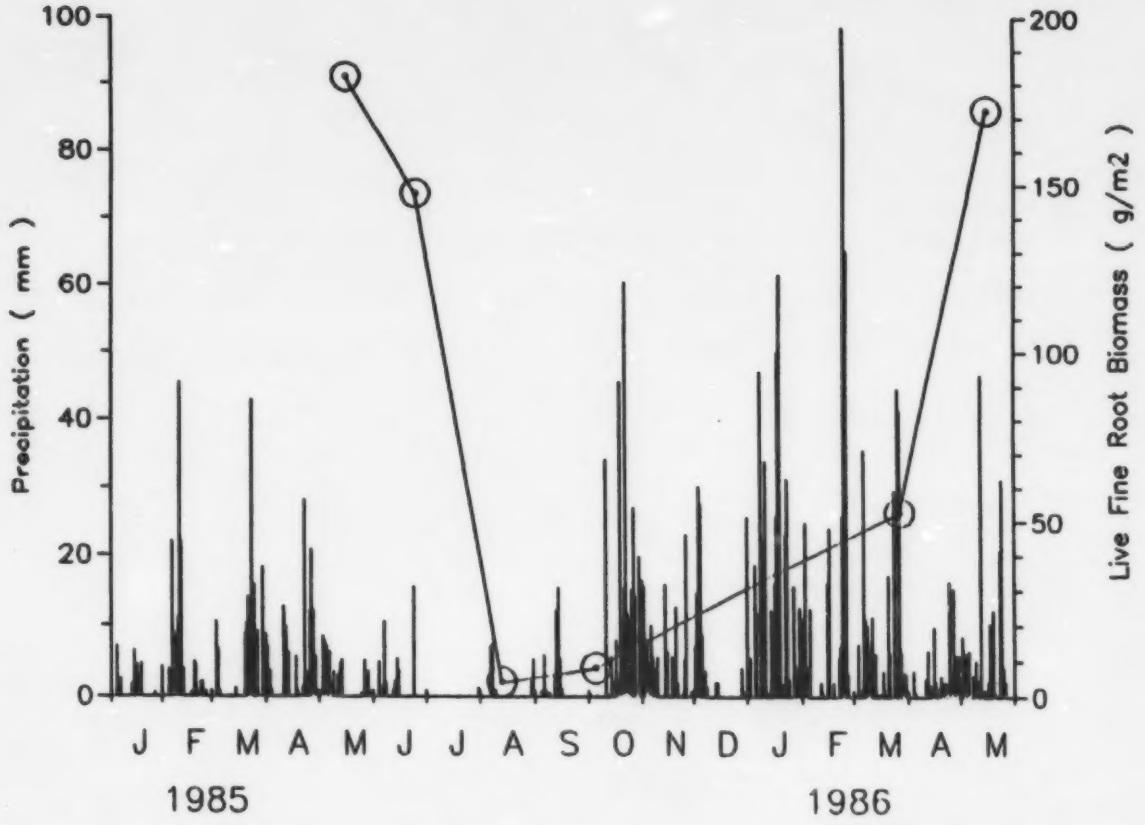

Figure 4.6 Daily precipitation at the Cowichan Lake Research Station for 1985 and the first six months of 1986 and the live fine root biomass at Stand E approximately 1 km from the climate station. (Precipitation data from B.C. Forest Service Cowichan Lake Research Station).

These periods of extreme drought may explain why so few live fine roots were found at Stand E at both the August and the October sampling dates. This rich lower slope stand receives seepage for most of the year (pers. observation), but the soil was very dry to a depth of 50 cm at the August and October 1985 sampling dates.

4.3.4 Seasonal dynamics of fine roots by soil layer

The seasonal dynamics of live and dead fine roots showed similar trends in the three soil layers which were sampled. The amplitude of the changes, however, differed between horizons. Figures 4.7 and 4.8 show fine root biomass for live and dead roots respectively, separated by horizon. The greatest change in fine root biomass occurred in the forest floor layer. The amplitude of the seasonal changes decreased with increasing depth in the soil for both live and dead fine root biomass.

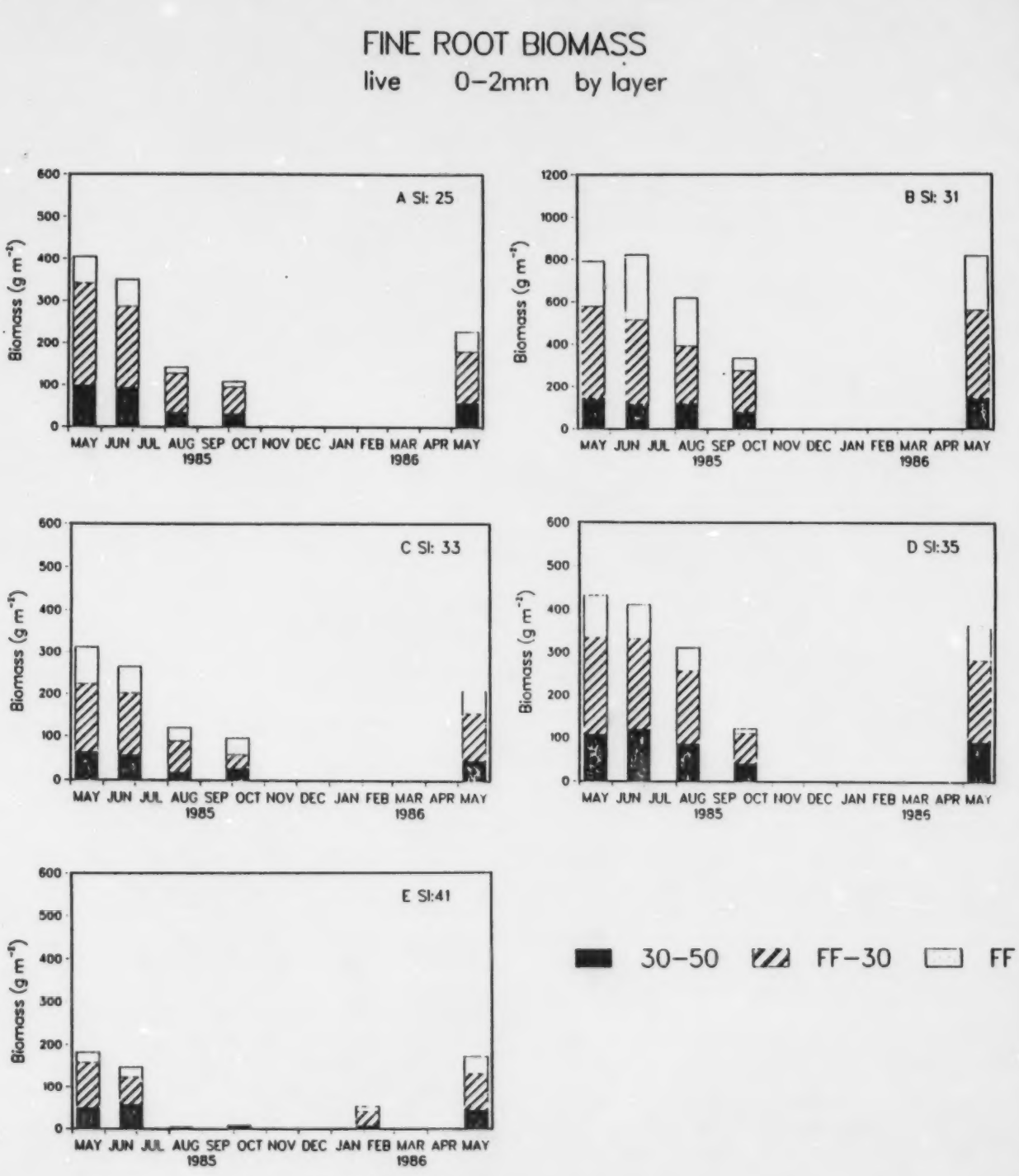

Figure 4.7 The proportion of live fine root biomass in the three soil layers at each of the five study sites.

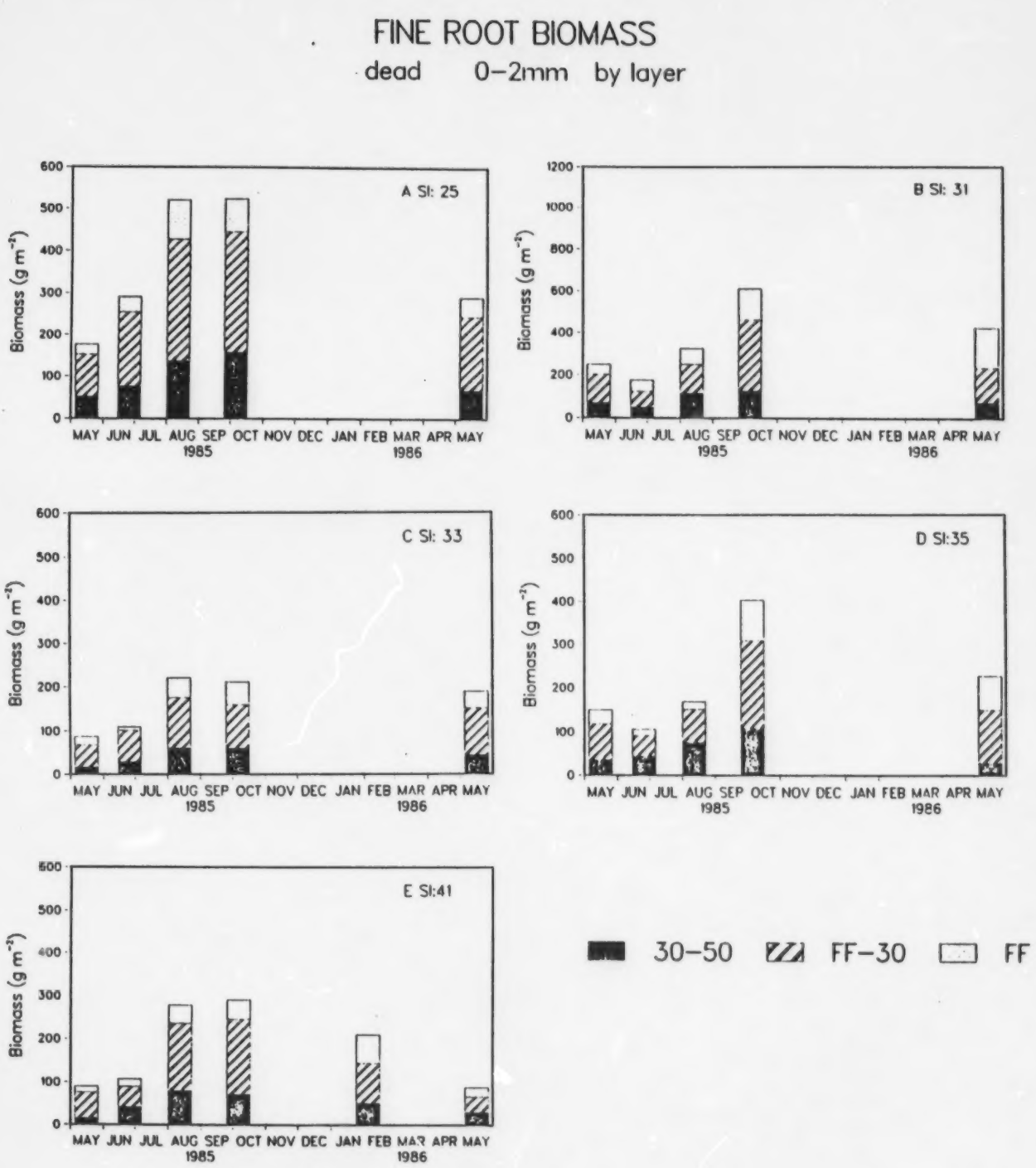

Figure 4.8 The proportion of dead fine root biomass in the three soil layers at each of the five study sites.

4.3.5 Seasonal dynamics of total fine root biomass

The sum of live plus dead fine root biomass yields total biomass as shown in Figure 4.9. There is little seasonal change in the total fine root biomass of the five study sites, but considerable variation in the ratios of dead to live fine roots. This result emphasizes the importance of separating live and dead categories when determinig fine root biomass. In addition to the points already raised in the Methods section and also in Appendix 1, failure to separate live from dead fine roots will contribute to error in production estimates which were derived from standing biomass data only.

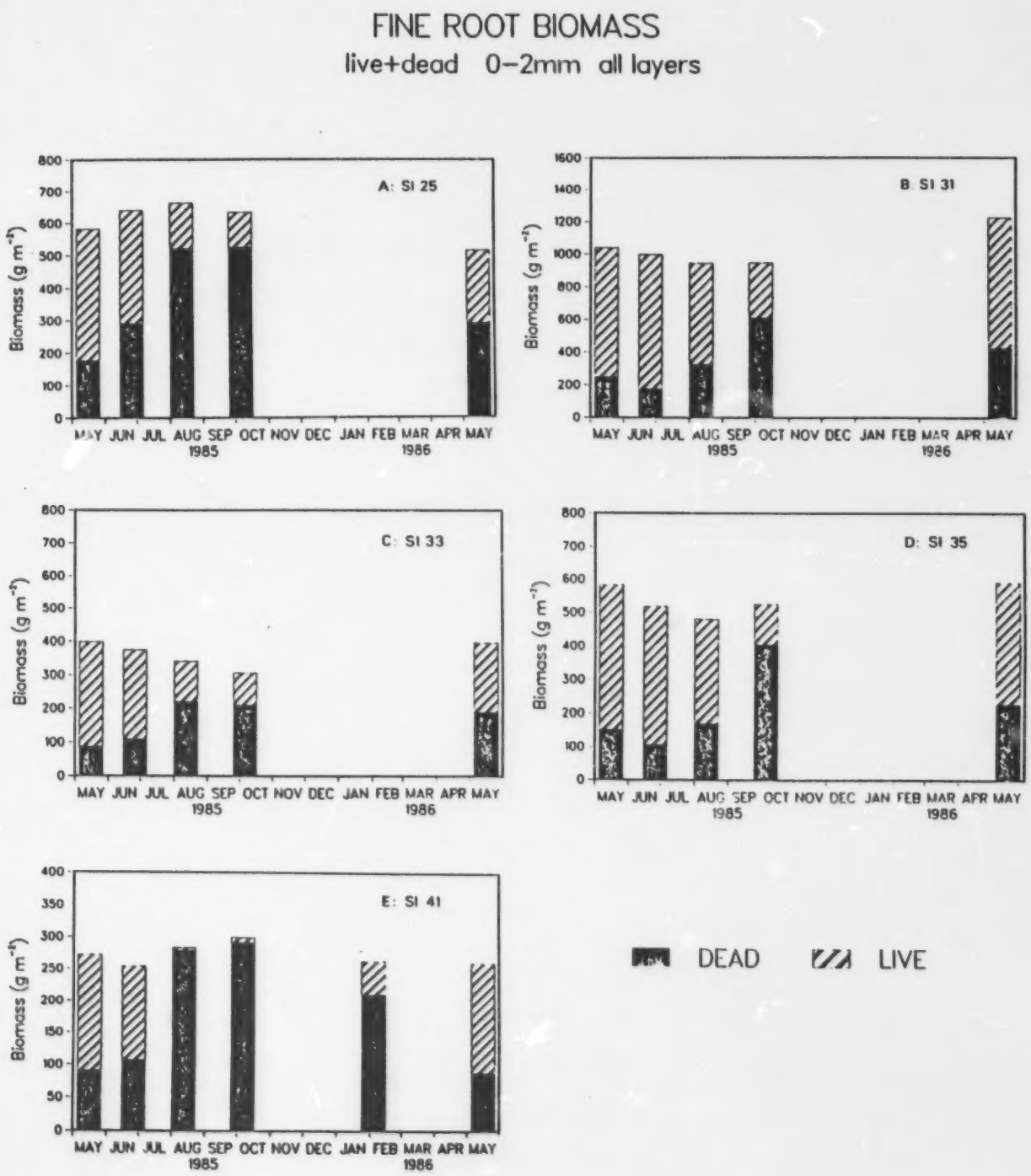

Figure 4.9 Total (live plus dead) fine root biomass at each of the five study sites.

Ratios of live to dead fine root biomass varied greatly between stands and also between the May 1985 and May 1986 sampling dates. The ratios ranged from 2.0 to 3.6 in May 1985, decreased sharply (0.03 to 0.6) in the summer and increased again (0.8 to 2.0) in May 1986.

A comparison of the change in live and dead fine root biomass from May 1985 to May 1986 is particularily interesting. Figure 4.10 shows live and dead fine root biomass expressed as a percentage of May 1985 values (=100%).

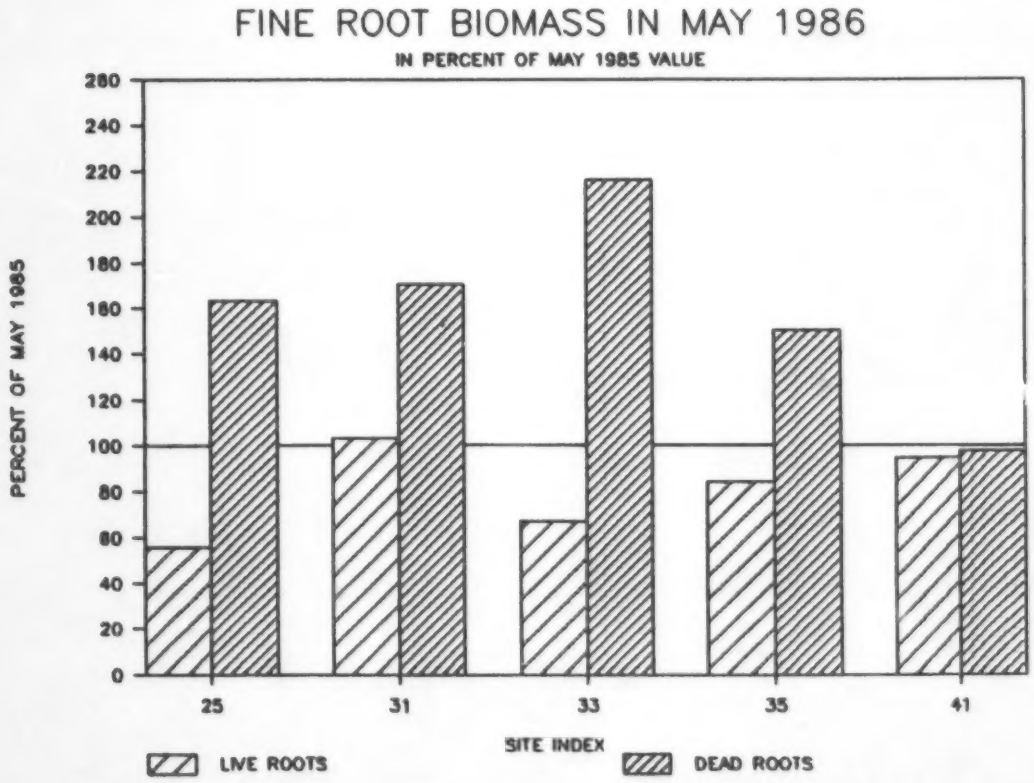

Figure 4.10 Live and dead fine root biomass in May 1986 expressed as the percentage of the May 1985 values. The five stands are ranked by site index.

In Stand A, the stand with the lowest site index, total fine root biomass was 12% lower in May 1986 than in May 1985. Live fine root biomass represented only 56% of the May 1985 value, while dead roots represented 163%. The drought of the summer 1985 was associated with a high mortality of fine roots, and by May 1986 live fine root biomass had not yet recovered and dead roots had not yet decreased to the May 1985 levels. Stand E, the site with the highest site index, showed a very different pattern. Live, dead and total biomass in May 1986 reached almost the same quantities as in May 1985 (95%, 97%, and 96%, respectively). The recovery of live fine root biomass occurred within seven months, mostly during the spring months (Figure 4.4). In Stand B, May 1986 live fine roots had reached the levels of May 1985 (103%), while dead fine roots had not yet decreased to the May 1985 level (171%). Live root biomass in stands C and D recovered to 67% and 84% of the 1985 values, respectively. Dead root biomass in both stands represented 216% and 150% of the quantities in May 1985.

Figures 4.9 and 4.10 illustrate how fine root biomass in the five stands was affected by a severe summer drought. The Figures also show how the stands differ in their capacity to re-establish fine roots and in the rates of disappearance of dead fine root biomass.

4.3.6 Seasonal dynamics of small (2-5 mm) root biomass

The seasonal dynamics of live and dead small (2-5 mm) root biomass are shown in Figure 4.11 for all five stands. Live small roots showed a pattern similar to that of fine roots, with the annual maxima in May and the annual minimum in either August or October. Live small root biomass in May 1985 ranged from 410 g/m^2 in Stand B to 60 g/m^2 in Stand E. Intermediate values were observed in Stands A, C, and D with 239, 108 and 226 g/m^2, respectively.

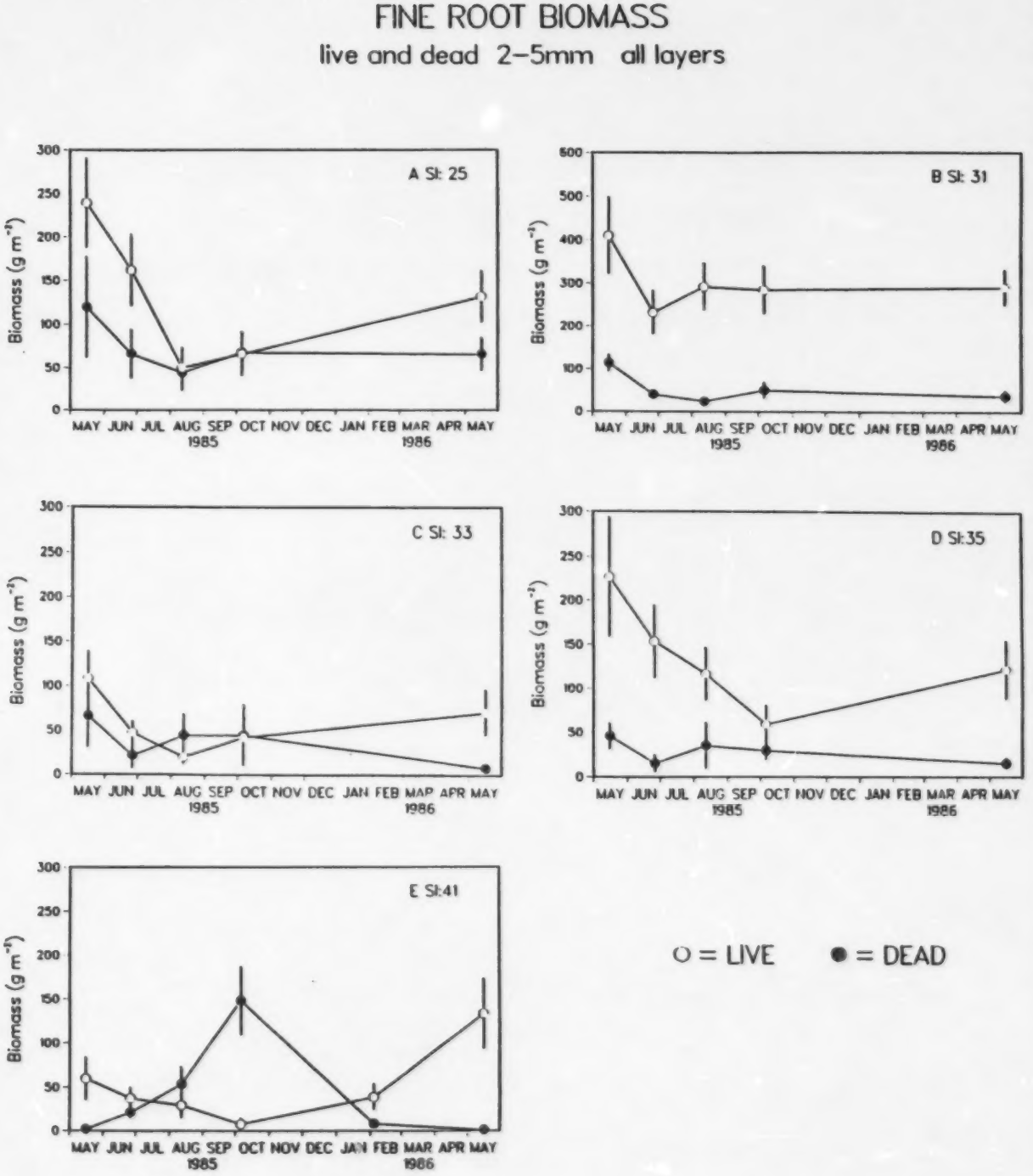

Figure 4.11 Seasonal dynamics of live and dead small root biomass for each of the five stands. Vertical bars represent ± 1 one standard error.

Results from the February sampling date, which was processed for Stand E only, suggest that most of the increase in live small roots occurred in the spring months, as was observed in the fine root component. Unlike the dead fine roots, however, most of the decrease in dead small roots in Stand E occurred from October to February.

The symmetry which was observed in the pattern of live and dead fine root biomass (i.e. decrease in live roots accompanied by an increase in dead roots) is not evident in the small root component. Stands A through E show a decrease in both live and dead small root biomass from May to June 1985. The observed high value for dead small root biomass in October in Stand E is particularly surprising, because none of the 3 preceding sampling dates indicated that such a quantity of live small roots was present.

Live small root biomass in May 1985 was lower than in May 1985 in 4 of the 5 stands. Only Stand E was able to re-establish its small root biomass to the previous year's level.

4.3.7 Non-coniferous root biomass

This category includes both live and dead roots of all diameter classes (cf. Methods). Non-coniferous roots are from understory species, with a single exception: Stand E contained one big-leaf maple (*Acer macrophyllum* Pursh). Most

of the non-coniferous roots were in the 0-2 mm diameter range. Larger diameters were encountered when salal and fern rhizomes were included in a sample.

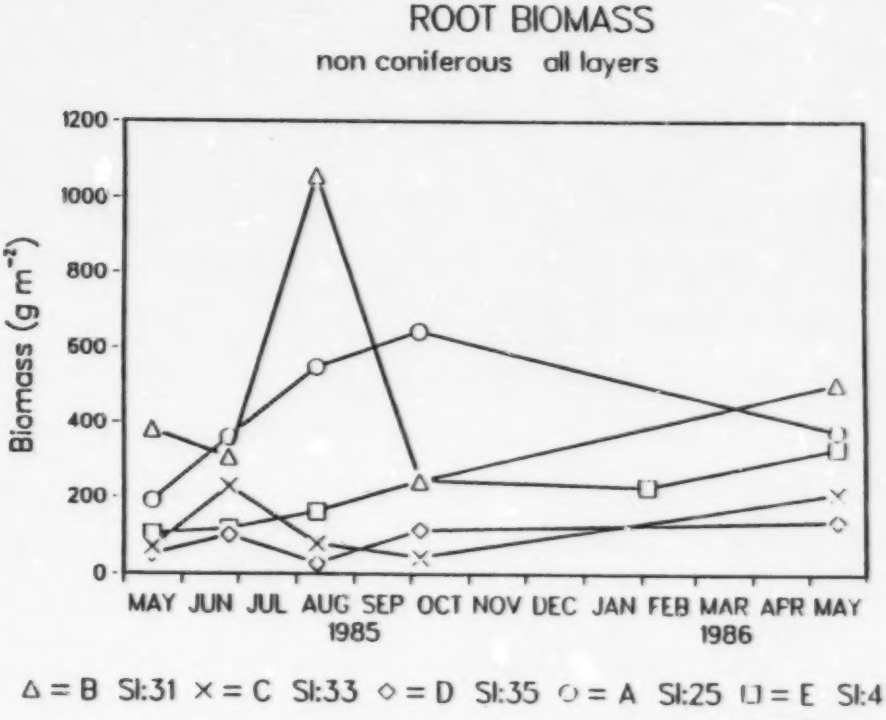

Figure 4.12 Seasonal dynamics of non-coniferous root biomass in the five study sites.

Figure 4.12 presents the seasonal pattern of non-coniferous root biomass. As with coniferous roots, there were large differences in biomass between stands. The seasonal dynamics of non-coniferous roots are more pronounced than the dynamics of the live plus dead coniferous fine root component. The maximum non-coniferous biomass was encountered during different sampling months in the five study sites. Root biomass of the understory vegetation of Stand B, which consisted of dense salal and

mahonia, peaked during August 1985. Stand D, which has fairly sparse understory vegetation, had the lowest amount of non-coniferous root biomass throughout most of the year.

4.4 Fine Root Production

4.4.1 Calculating production and mortality estimates

Estimates of fine root production and mortality are commonly derived from the observed seasonal changes in live and dead fine root biomass (Moir and Bachelard 1969, Santantonio and Hermann 1985, Vogt *et al.* 1980). The potential systematic error which may be inherent in this approach was mentioned in the Methods section and was discussed in detail by Kurz and Kimmins (in press) (cf. Appendix 1).

As was shown in the preceding section on seasonal dynamics of fine root biomass, there appears to be a sharp decline in live coniferous fine roots in the summer months, possibly induced by moisture stress. For the calculation of fine root production and mortality estimates, it had to be assumed that each observed change in live root biomass during a sampling interval was solely due to either production or mortality and that the two processes did not occur simultaneously. This assumption is probably not fully satisfied, particularly during the period from October 1985

to May 1986. It is currently unknown, however, whether a coniferous fine root has an inherent lifespan, and if such a lifespan does exist, it is not known how long it might be. Factors which may induce fine root mortality are also poorly understood and require additional research.

The second assumption which had to be made for the estimation of annual production and mortality was that no additional peak or trough in either live or dead root biomass occurred between the sampling dates. This assuption is particularly critical for the fall and winter months from October to May. The October samples were taken only a few days before the fall rains started (cf. Figure 4.6). If moisture stress is in fact the cause of fine root mortality, this would suggest that we sampled at or close to the point at which live fine root biomass was at its annual low.

Although samples were collected in November, February and March for all five study sites, we were unable to process those samples due to time and financial constraints. We managed to process the February samples for Stand E and, as discussed before, the results support the assumption that no additional peaks in either live or dead fine root biomass occurred.

Violating either of the two assumptions mentioned above would lead to an underestimate of the actual production and mortality. Thus, the estimates reported below are probably conservative.

Three commonly used methods, based on "All Changes" (AC), "Significant Changes" (SC) and the "Decision Matrix" (DM), were selected to calculate fine root production and mortality estimates. All three methods are described in detail in Section 3.7. (Methods).

Fine root density decreases with greater soil depth, and roots in different layers are subject to different environmental conditions (e.g. nutrient and moisture availability, temperature, etc.). Figures 4.7 and 4.8 showed that changes in fine root biomass were greater in the forest floor than in the 30-50 cm layer. It may therefore be necessary to treat the fine roots in each soil layer as separate populations for which specific production and mortality rates are estimated. Similarly, the roots in the 0-2 mm diameter class should perhaps be divided into two populations representing the 0-1mm and the 1-2 mm diameter ranges.

The data on 0-2 mm diameter fine roots can be combined in four different ways (Figure 4.13). Production and mortality estimates of fine roots were calculated for each of those four groupings.

		DIAMETER	
		0-2 mm	0-1 + 1-2 mm
HORIZON	FF-50	I	II
	FF 0-30 30-50	III	IV

Figure 4.13 Four different groupings of fine roots in the 0-2 mm diameter class found in the top 50 cm of the soil.

The Type I grouping treats fine roots in the 0-2 mm diameter class and in the FF-50 cm depth range as a single population. The Type II grouping separates the diameter classes 0-1 mm and 1-2 m into two populations and treats the FF-50 cm soil profile as one layer. The Type III grouping separates the roots according to their soil layer of origin but maintains only one diameter class. The Type IV grouping treats the two root diameter classes separately in each of the three soil layers. In each case, the annual estimates for production and mortality are the sum of the estimates for each population.

The ability to identify differences in the seasonal patterns in both the diameter classes and the soil layers

increases from the Type I grouping to the Type IV grouping. This can be advantageous if, for example, a decrease in the biomass of the 0-1 mm diameter class in the forest floor occurs during the same interval as an increase in the 1-2 mm root biomass in the 30-50 cm layer. The Type I grouping would not be able to detect these changes. These opposing trends can be identified by the Type IV grouping and production and mortality can be estimated accordingly. On the other hand, as the number of independent estimates increases from Type I to Type IV, so does the number of error terms associated the estimates of the annual totals.

Type	Decision Matrix		All Changes		Significant Changes (p=0.05)	
PRODUCTION						
I	100		100		100	
II	131.8	(20.8)	106.0	(6.8)	87.4	(34.8)
III	123.0	(23.7)	106.4	(7.5)	95.8	(5.8)
IV	154.8	(23.3)	120.2	(17.9)	78.6	(32.9)
MORTALITY						
I	100		100		100	
II	113.8	(11.0)	103.2	(3.1)	103.2	(3.1)
III	127.2	(23.0)	104.8	(6.1)	100.6	(5.6)
IV	140.0	(15.4)	111.8	(8.1)	101.4	(8.9)

Table 4.6 The effects of four types of groupings on fine root production and mortality estimates expressed as a percentage of the estimate obtained for Type I. See Figure 4.13 for an explanation of the four types. Data represent the mean (standard deviation) based on all five stands for each of the 3 computational methods.

Separating fine roots into four different groupings had different effects on production and mortality estimates depending on the computational method which was applied. For a comparison of the effects of separating fine roots into groups according to diameter class and soil layer, the estimates obtained for the Type I grouping were used as reference (100%) and the remaining three Types were expressed as a percentage of the Type I estimate. Table 4.6 shows a comparison of the mean production and mortality

estimates and their standard deviations based on the results of the five stands.

The production and mortality estimates calculated with the decision matrix increased as a result of the separation of fine roots into different populations. The mean production estimates were 31.8%, 23.0% and 54.8% above the Type I grouping for groupings II, III and IV, respectively.

Production and mortality estimates calculated from all observed changes in live fine root biomass were less affected by the separation of roots into different populations. Mean production estimates for Type II, III, and IV were 6.0%, 6.4% and 20.2% above those of Type I. For some stands, no change was observed and a 1% decrease was obtained once.

The separation of fine roots into different populations caused a reduction in production estimates if these were based on only significant changes in live fine root biomass. The mean production estimates were 12.6%, 4.2% and 21.4% below the Type I estimate for Types II, III, and IV, respectively. Note, however, that these are average responses for the five stands. For individual stands, production estimates ranged from 20% above to 72% below the Type I estimate. Mortality estimates based on significant observed changes in live fine root biomass were much less affected by the separation of fine roots into groups.

These reductions in estimates for the SC computational method are due to the fact that seasonal changes in individual populations may not be significant. The increase in fine root biomass from the low in the summer of 1985 to the high in the spring of 1986 in stand A, for example, was not significant if the roots were separated into 2 diameter and/or 3 soil layer classes.

The largest differences between groupings for each of the three computational methods were between Types I and IV. The Type I grouping produces the most conservative estimates for the DM and AC computational methods, but it produces the highest estimates for the SC computational method. For reasons discussed above, i.e. the possible masking of true trends by opposing changes in the biomass of different diameter classes, the Type I grouping of fine root data may not be the most accurate in all cases. It has been used widely in fine root production studies, however, and will also be used for the remainder of this report.

4.4.2 Fine root production and mortality estimates

For the computations in this section, the fine roots in the 0-2mm diameter class and in the forest floor to 50 cm soil layer have been treated as one population, i.e. all calculations are based on a Type I grouping. The estimates are based on ash-free dry weights and are reported in g/m^2.

To obtain Mg/ha (i.e. t/ha) values divide the g/m^2 values by 100.

Fine root production and mortality estimates based on three different computational methods for each of the five stands are reported in Table 4.7. For a comparison of the effects of the three computational methods, the same estimates have also been expressed as a percentage of the estimate obtained from the SC computational method (Table 4.8).

		PRODUCTION (g/m^2)			MORTALITY (g/m^2)		
Stand	SI	DM	AC	SC	DM	AC	SC
A	25	199	118	118	378	296	296
B	31	514	512	481	490	487	487
C	33	112	112	112	215	215	215
D	35	287	242	242	356	311	311
E	41	208	168	168	218	178	178

Table 4.7 Annual fine root production and mortality (g/m^2) for the five stands calculated with three computational methods: decision matrix (DM), all changes (AC) and significant changes (SC). See text for explanation of methods.

Stand	SI	PRODUCTION (g/m^2)			MORTALITY (g/m^2)		
		DM	AC	SC	DM	AC	SC
A	25	168.6	100.0	100.0	127.7	100.0	100.0
B	31	106.94	106.4	100.0	100.6	100.0	100.0
C	33	100.0	1[illegible].0	100.0	100.0	100.0	100.0
D	35	118.6	100.0	100.0	114.5	100.0	100.0
E	41	123.8	100.0	100.0	122.5	100.0	100.0
Mean S.D.		123.6 (26.9)	101.3 (2.9)	100.0	113.1 (12.6)	100.0	100.0

Table 4.8 Annual fine root production and mortality (g/m^2) for the five stands expressed as a percentage of the estimates obtained from the SC computational method.

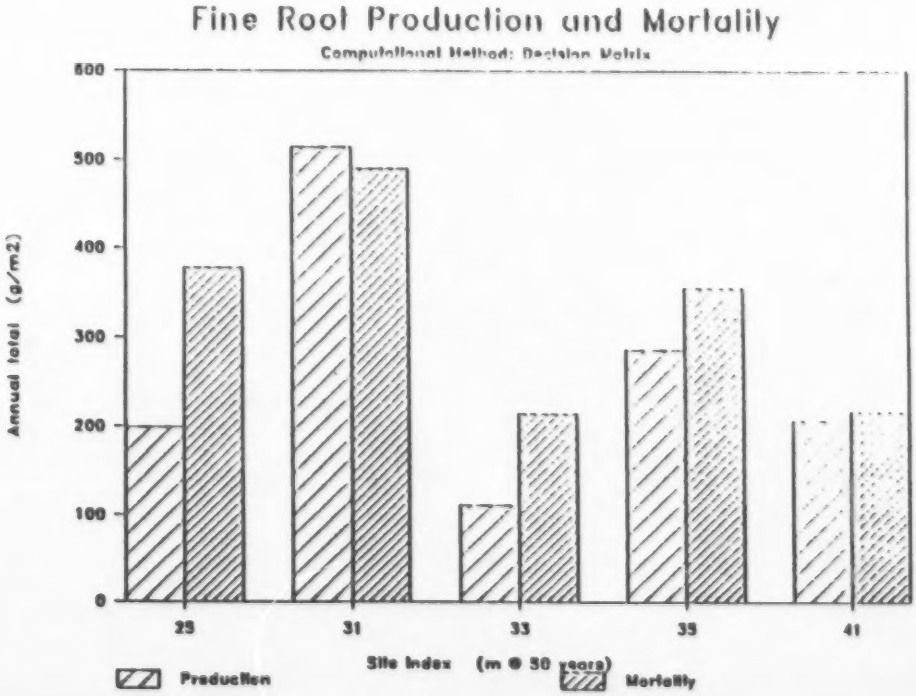

Figure 4.14 Estimates of fine root production and mortality for each of the five stands based on the decision matrix.

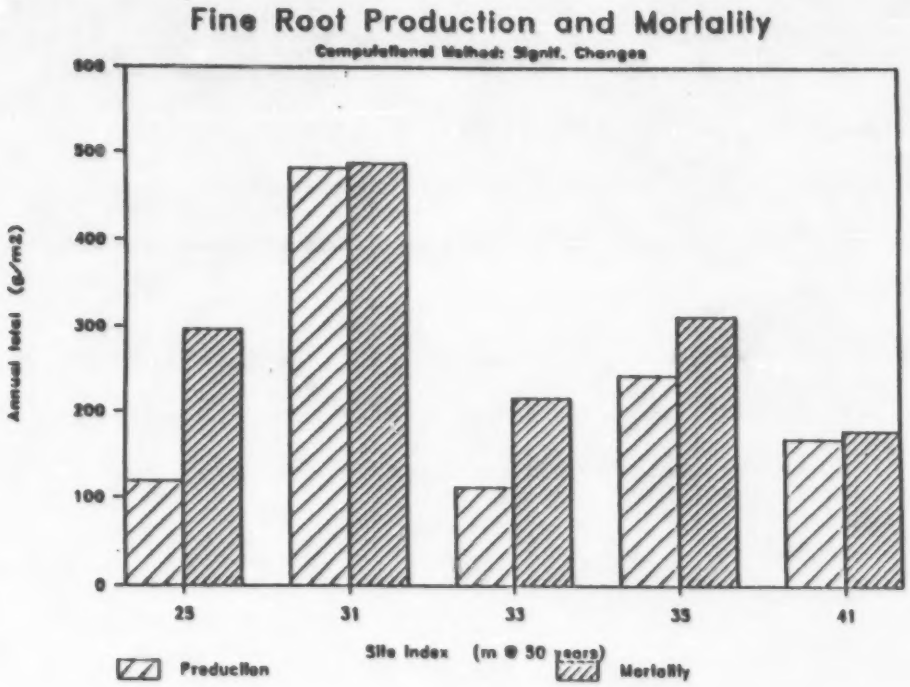

Figure 4.15 Estimates of fine root production and mortality for each of the five stands based on observed significant changes in live fine root biomass.

Production estimates obtained from the AC and the SC method were identical with one exception: in Stand B the AC method calculated 6.4% more production than the SC method. Estimates based on the decision matrix were on average 23.6% higher than the estimates obtained from the SC method. Mortality estimates based on both the AC or the SC method were identical, while these based on the decision matrix were on average 13.1% higher.

As discussed in the preceding section, separation of fine roots into different populations according to diameter class and soil layer has different effects on production and

mortality estimates depending on the computational method used. Consequently, the statement that the AC and SC computational methods yielded similar estimates cannot be generalized. Differences between the AC and SC methods were small in this study because the sampling frequency was low. The sampling intervals were large enough to show a clear seasonal trend with significant differences between the peaks and troughs in live and dead fine root biomass.

The estimates of annual production and mortality of fine roots differed between stands (Table 4.7, Figures 4.14 and 4.15). Production in Stand B was 481 g/m^2 and 514 g/m^2 based on the SC and DM method, respectively. This was over four times higher than in Stand C, which had a production of 112 g/m^2 for all computational methods.

Based on the DM computational method, the stands with the lowest (Stand A) and highest (Stand E) site index, had 199 g/m^2 and 208 g/m^2 of fine root production. The SC computational method yielded lower estimates and showed larger differences between the two stands: 118 g/m^2 and 168 g/m^2 for Stands A and E, respectively. Production estimates for Stand D were the second highest and ranged from 287 g/m^2 for the DM method to 242 g/m^2 for the SC method.

Estimates of annual fine root mortality also differed between the five stands, but they covered a narrower range than the production estimates. Based on the DM method, mortality estimates are lowest for stands C and E, 215 g/m^2

and 218 g/m^2, respectively. The SC method calculated the lowest mortality estimates for Stand E (178 g/m^2) and yielded the second lowest estimate for Stand C (215 g/m^2). The highest mortality estimates, obtained for Stand B, range from 490 g/m^2 to 487 g/m^2 for the DM and SC method, respectively.

Figures 4.14 and 4.15 present a comparison of fine root production and mortality in each stand. Only in Stands B and E were the two estimates approximately equal. Mortality estimates in Stands A and C were approximately double the production estimates. In Stand D, production represented about 80% of mortality. These differences between production and mortality estimates are explained by the lower fine root biomass in May 86 compared to that in May 1985 (cf. Figure 4.10). The lower fine root biomass in May 1986 may be due to the heavy mortality which occurred during the unusually dry summer of 1985 and the inability of some stands to re-establish the fine root biomass by the following spring.

4.4.3 Turnover rates of fine root biomass

The differences in fine root production and mortality estimates between stands are to some extent due to the differences in maximum fine root biomass. When production and mortality estimates are expressed in relation to the quantity of fine roots present in May 1985, a different

picture emerges. The ratios of annual production : biomass in May 1985, and annual mortality : biomass in May 1985 are shown in Figures 4.16 and 4.17 and in Table 4.9.

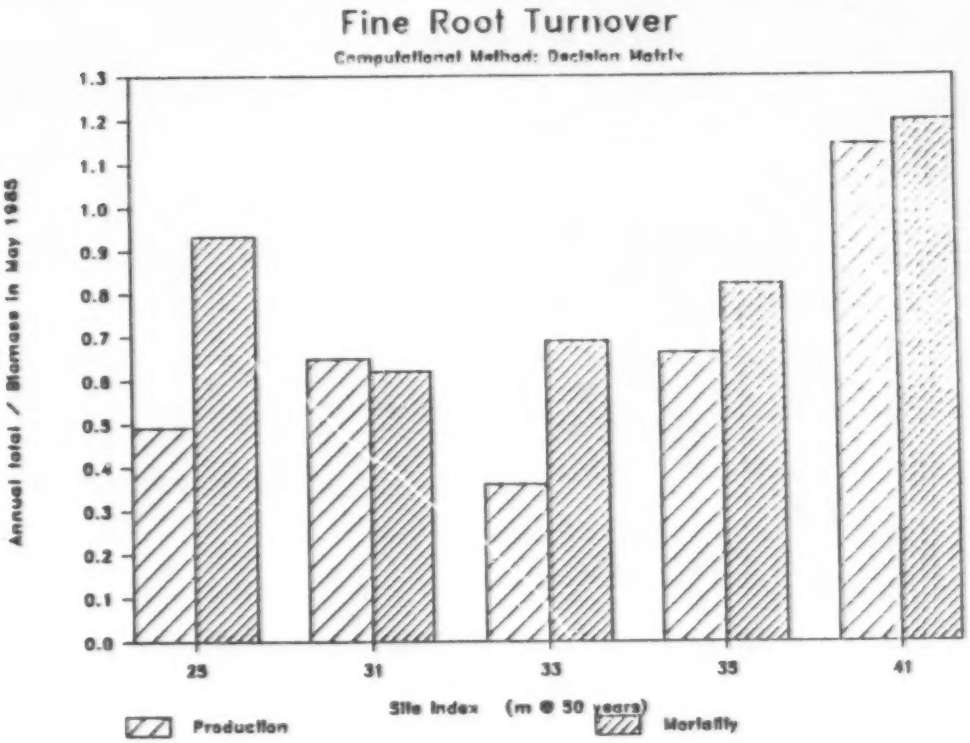

Figure 4.16 Fine root production and fine root mortality based on the decision matrix, divided by the live fine root biomass in May 1985, for each of the five stands.

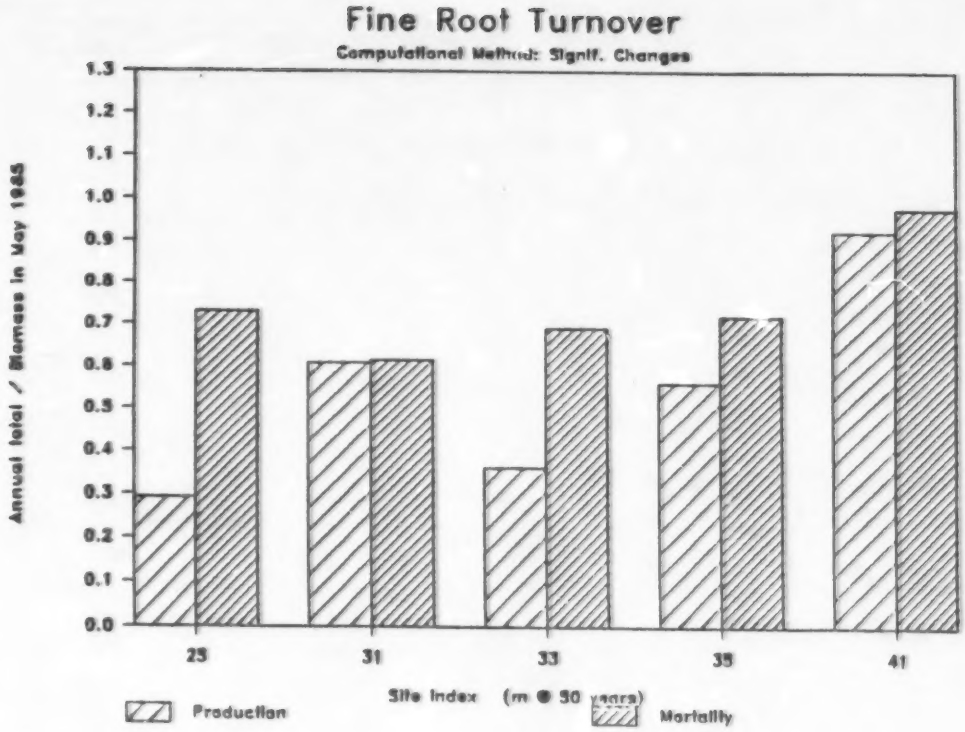

Figure 4.17 Fine root production and fine root mortality based on the SC method divided by the live fine root biomass in May 1985, for each of the five stands.

STAND	SI	BIOMASS MAY 85	PRODUCTION/BIOMASS			MORTALITY/BIOMASS		
			DM	AC	SC	DM	AC	SC
A	25	404.9	0.49	0.29	0.29	0.93	0.73	0.73
B	31	791.5	0.65	0.65	0.61	0.62	0.62	0.62
C	33	311.2	0.36	0.36	0.36	0.69	0.69	0.69
D	35	432.5	0.66	0.56	0.56	0.82	0.72	0.72
E	41	182.0	1.14	0.92	0.92	1.20	0.98	0.98

Table 4.9 The ratios of annual fine root production : fine root biomass in May 1985 and annual fine root mortality : fine root biomass in May 1985. Production and mortality estimates are based on three computational methods which are described in the text.

These ratios represent a measure of turnover. A ratio of 0.5 for both processes (production and mortality) implies that 50% of the fine root biomass in May 85 had died and was replaced by May 1986. The inverse of the turnover rate of 0.5 implies that the mean life span of a fine root is two years (Table 4.10).

STAND	SI	BIOMASS MAY 85	LIFE SPAN (years) (PRODUCTION)			LIFE SPAN (years) (MORTALITY)		
			DM	AC	SC	DM	AC	SC
A	25	404.9	2.03	3.43	3.43	1.07	1.37	1.37
B	31	791.5	1.54	1.55	1.65	1.62	1.63	1.63
C	33	311.2	2.78	2.78	2.78	1.45	1.45	1.45
D	35	432.5	1.51	1.79	1.79	1.21	1.39	1.39
E	41	182.0	0.88	1.08	1.08	0.83	1.02	1.02

Table 4.10 Estimates of mean life span of fine roots in years, based on annual production and mortality estimates. These values are the inverse of the data presented in Table 4.9.

The turnover rates were higher when based on mortality estimates than when based on production estimates, with a single exception: in Stand B the decision matrix calculated a slightly higher turnover rate based on production (Table 4.9). Turnover rates based on mortality (DM method) range from 0.62 for Stand B to 1.2 for Stand E, while those calculated from the SC method range from 0.62 to 0.98 for Stands B and E, respectively (Table 4.9). These rates imply fine root life spans of 0.83 to 1.63 years (Table 4.10).

Turnover rates based on estimates of production cover a wider range. The decision matrix calculated a low of 0.36 for Stand C and a high of 1.14 for Stand E. The SC method also computed the highest rate for Stand E (0.92) but it

calculated the lowest value for Stand A (0.29) (Table 4.9). The mean life spans for fine roots which result from these turnover rates range from 0.88 years in Stand E to 3.4 years in Stand A (Table 4.10).

Based on the SC method the turnover rates imply that 62% to 73% of the live fine roots in Stands A through D had died during the sampling period. Stand E, the lower slope sword-fern Stand, experienced 98% mortality of its live fine roots but it was able to replace most of the roots by the following May.

A comparison of the absolute and relative mortality of fine roots in Stands B and E shows that in Stand B about 480 g/m^2 of fine roots died, which was twice as much as in Stand E (218 g/m^2 for DM, 178 g/m^2 for SC). In Stand B this amount represented only 62% of the fine root biomass in May 85, but in Stand E it represented 120% (DM) and 98% (SC) of the live fine root biomass in May 85. The difference in relative and absolute mortality rates between Stand E and the other four stands suggests that Stand E was more affected by the summer drought of 1985.

4.4.4 Site quality and fine root production

Many factors determine the "quality" of a site and there has been much discussion in the literature about an appropriate measure of site quality (cf. Hagglund 1981). For

this study, the two available measures of site quality are site index (meters at breast-height age 50) (Bruce 1981) and nitrogen mineralization rates. Several variables describe fine root production and the issue is complicated by the lack of an agreed-upon method of determining and calculating fine root production, as discussed above.

	SI		N_{min}-FF		N_{min}-MS	
	r	p	r	p	r	p
$PROD_{DM}$	-.107	.864	-.361	.551	-.484	.409
$PROD_{SC}$	-.022	.972	-.329	.589	-.377	.532
$MORT_{DM}$	-.569	.316	-.679	.190	-.858	.063
$MORT_{SC}$	-.465	.430	-.673	.213	-.739	.153
TURN-$PROD_{DM}$	.757	.138	.779	.120	.533	.355
TURN-$PROD_{SC}$	.857	.063	.738	.155	.599	.286
TURN-$MORT_{DM}$	.481	.412	.784	.116	.506	.384
TURN-$MORT_{SC}$	.690	.197	.917	.028	.726	.165

Table 4.11 The relationships between site index, nitrogen mineralization in the forest floor and in the mineral soil and several measures of fine root production and mortality. Two different computational methods (DM and SC) are used. All relationships are based on the data from all five stands.

Table 4.11 lists correlation coefficients and significance levels for the relationships between site index, N_{min} in the forest floor, and N_{min} in the mineral

soil and several measures of fine root production (PROD), mortality (MORT), and turnover (TURN).

Most of the correlations were not significant. N_{min} in the forest floor and turnover rate based on the estimate of fine root mortality calculated from the SC method (TURN-$MORT_{SC}$) were highly positively correlated (p=.028). Turnover based on an estimate of production, as determined by the SC method (TURN-$PROD_{SC}$) was significantly (p=0.063) and positively correlated with site index. Fine root mortality, based on the DM method, was significantly (p=0.063) and negatively correlated with the N_{min} rate in the mineral soil.

Although most of the correlations between any measure of site quality and any measure of production or mortality were not significant, they all showed a negative correlation. With increasing site quality both fine root production and mortality tended to decline. In contrast, all three measures of site quality were always positively correlated with all four measures of turnover, though most of the relationships were not significant.

A fine root production estimate of 112 g/m^2 (Stand C) is equal to 1.12 t/ha of site production. Assuming a specific gravity for Douglas-fir stemwood of 0.45 g/m^3 (Megraw 1986), this fine root biomass is equal to 2.5 m^3/ha of stemwood. Fine root biomass production (based on the SC

method) in Stands A, B, D, and E is equal to 2.6, 10.7, 5.4, and 3.7 m^3/ha of stemwood, respectively.

The ultimate question, however, still remains unanswered: "Does the proportion of the total net primary production allocated to fine root production change with site quality?" The five stands of this study have been selected to cover a range of site indices. Above-ground net primary production differs in the five stands. The data to determine above-ground net primary production have been collected for the larger study (Kurz, in prep.) of which this study was a part. Analysis of the above-ground net primary production data has not yet been completed.

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6. APPENDICES

APPENDIX 1

Manuscript of Kurz and Kimmins (in press).

Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach

Werner A. KURZ and James P. KIMMINS

Faculty of Forestry
The University of British Columbia
2357 Main Mall
Vancouver, B.C., V6T 1W5
Canada

ABSTRACT

KURZ, W.A. and J.P. KIMMINS. 198_. Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach. Can. J. For. Res. submitted.

Fine root production rates are most commonly calculated from periodic measurements of live and dead fine root biomass. The accuracy of production estimates based on this method is very sensitive to violations of the inherent assumptions, particularly the assumption that the processes of fine root production and mortality are temporally separate.

A simple model was used to simulate data for a variety of seasonal patterns of live and dead fine root biomass. Fine root production and mortality rates were calculated from these simulated data using two different computational methods. Comparison of the calculated rates with the known rates (the rates used to generate the seasonal patterns) revealed that violations of the above assumptions can result in inaccurate rate estimates. When fine root production and mortality occur simultaneously within a sampling interval, the calculated production rate will greatly underestimate the true value.

Additional error in the rate estimates may result from sampling error associated with the fine root biomass data. The model suggested that sampling error can cause either overestimation or underestimation of fine root production.

INTRODUCTION

Fine root production is an important component of both nutrient and carbon cycles in forest ecosystems (Vogt et al. 1986b; McClaugherty et al. 1982). The most commonly used method of estimating fine root production and mortality involves periodic measurements of live, and in some cases dead, fine root biomass. The observed changes of fine root biomass are the basis for the calculation of production and mortality rates. (Persson 1978; McClaugherty et al. 1982; Fairley and Alexander 1985).

Recent publications have addressed the questions of sample size and sampling error (Persson 1978; Singh et al. 1984), the timing of the sampling to capture the peaks and troughs in standing fine root biomass (Vogt et al. 1986a), and the computational methods used to calculate fine root production (McClaugherty et al. 1982; Fairley and Alexander 1985). However, the consequences of failing to satisfy the assumptions on which the computational methods are based have not been examined in detail. One particularly important assumption is that the processes of production and mortality are temporally separate. This assumption is frequently not satisfied, because in many climates both production and mortality of

fine roots occur within a single sampling interval, and the observed change in live fine root biomass is the combined result of those two processes. Failure to account for the concurrence of these processes may lead to a substantial underestimate of fine root production.

The objectives of this paper are 1, to analyse the potential magnitude of the error in production rate estimates caused by the concurrence of production and mortality and by the sampling error associated with fine root biomass estimates, and 2, to compare the accuracy of two computational methods which are commonly used to estimate production and mortality from seasonal fine root biomass data.

METHODS

A simple computer model was used to generate monthly biomass values of live and dead fine roots from given production, mortality and decomposition rates. The model has three rate variables, Production (PROD), Mortality (MORT) and Disappearance (DISA), and two state variables, Live Fine Roots (LFR) and Dead Fine Roots (DFR). The transfers to and from the state variables are

[1] $PROD_{t+1} = BPR * PR_{t+1}$

[2] $MORT_{t+1} = LFR_t * MR_{t+1}$

[3] $DISA_{t+1} = (DFR_t + MORT_{t+1}) * DR_{t+1}$

where PR, MR, and DR are monthly rates of production, mortality and disappearance, respectively. BPR is a dummy constant which serves as a multiplier of the monthly production rate. The user defines BPR, initial (t=0) values of LFR and DFR, and monthly values for the three rate variables. The model simulates monthly time steps and calculates for each month:

[4] $LFR_{t+1} = LFR_t + PROD_{t+1} - MORT_{t+1}$

[5] $DFR_{t+1} = DFR_t + MORT_{t+1} - DISA_{t+1}$

Twelve monthly time steps were simulated and monthly values for production and mortality were summed to give annual totals. These annual totals were compared with annual production and mortality estimates obtained from the simulated seasonal pattern of live and dead fine root biomass using two common computational methods (explained below).

In the first part of the analysis we assumed that the observer can determine live as well as dead fine root biomass without error. This implies also that the observer can accurately distinguish between live and dead fine roots. These assumption were necessary to assess the

effects of the concurrence of production and mortality on production estimates, independently of other sources of error. In the second part of the analysis, a Monte-Carlo simulation with 1000 runs was used to examine the potential effects of a 10% sampling error. In both parts of the analysis we assumed that the sampling dates coincide with the peaks and troughs of the seasonal pattern of fine root biomass.

Two computational methods were employed to calculate annual production and mortality of fine roots from the simulated pattern of live and dead fine root biomass.

Method I: Production was calculated as the sum of all observed increments in live fine root biomass (LFR). Mortality was calculated as the sum of all decrements in LFR.

Method II: Monthly values for production and mortality were calculated from the observed changes in both live and dead fine root biomass using the decision matrix and equations presented by Fairley and Alexander (1985) (cf. McClaugherty et al. 1982). The monthly values were summed to give annual totals.

RESULTS

1. Deterministic Simulations

The objective of our analysis was to assess the effects of various degrees of temporal concurrence of production and mortality of fine roots on the accuracy of two commonly used methods for the calculation of these parameters. The four example cases to be presented differ in the seasonal patterns of production and mortality. The two processes occur concurrently in 12, 0, 4, and 9 months in cases 1 through 4, respectively. For all four cases, disappearance is assumed to be constant (DR = 0.2/month).

CASE 1: Monthly production and mortality rates are constant and equal, leaving the system in steady state (i.e. constant fine root biomass). Figure 1-1 A shows monthly production and mortality and Figure 1-1 B presents the corresponding values of live and dead fine root biomass, which display no seasonal trend. Applying either of the computational methods to the biomass data yields production and mortality estimates of zero while the "true" rates which generated the biomass data are 12 Mg/ha/year (Table 1).

CASE 2: Values of PR and MR are chosen to represent seasonal dynamics with a complete temporal separation in production and mortality. At any one time step only production or mortality occurs, not both. Consequently, any observed increase in LFR is due solely to the effect of production, while any decrease in LFR is due only to mortality. DFR has seasonal additions through mortality and continuous outflow through disappearance. Figure 1-2 A presents the seasonal pattern of PROD and MORT and Figure 1-2 B displays the seasonal dynamics of live and dead fine root biomass. The seasonal course contains a pronounced maximum of LFR in the spring, a sharp decline in the summer, and a gradual increase in the fall and winter. Such a seasonal pattern has been observed in areas with mild winters and summer drought (Santantonio and Hermann 1985; Keyes and Grier 1981).

The "true" values for total production and mortality are 10.4 and 10.1 Mg/ha/year, respectively. Both computational methods yield estimates which represent 100% of "true" production and mortality (Table 1).

CASE 3: In this example, PR and MR are again seasonal but occur simultaneously during three spring months and one fall month. During those four months, the observed changes in LFR are due to the combined effects

of the two rate variables. The monthly values for PROD and MORT are represented in Figure 1-3 A and the corresponding seasonal development of LFR and DFR is illustrated in Figure 1-3 B.

The "true" values for total production and mortality are 10.4 Mg/ha/year. Using Method I to calculate total production and mortality from LFR yields 8.8 Mg/ha/year (84.5% of the "true" value) for both rates. Method II results in somewhat higher values: 9.1 Mg/ha/year (87.4%) for both production and mortality (Table 1). The simultaneous occurrence of production and mortality during four months of the year leads, in this example, to an underestimate of annual production by 15.5% and 12.6% by Methods I and II, respectively.

CASE 4: This case represents a situation with a continuous low-level mortality rate throughout much of the year, and an increased mortality rate during the summer months. Production is also seasonal, with intermediate rates in fall and winter, high rates in the spring and no production in summer. Thus, the rates which determine LFR occur simultaneously in 9 of the 12 months.

Figure 1-4 A shows production and mortality which result from these assumptions, and Figure 1-4 B

represents the associated patterns of LFR and DFR. "True" total production and mortality are both 10.4 Mg/ha/year. Method I computes production and mortality rates of 5.8 Mg/ha/year (55.4%). Method II yields 6.3 Mg/ha/year for both rates, which represents 60.6% of the "true" production and mortality estimates (Table 1).

2. Monte-Carlo Simulations:

The assumption that the observer can obtain an error-free measure of fine root biomass at each sampling date was replaced with the assumption that the observer can only measure fine root biomass within $\pm$ 10% of the true value. One thousand runs were simulated for each of the four cases. The means, standard deviations, and ranges of the estimates of annual rates of production and mortality, as obtained by the two computational methods and expressed in percent of the true values, are presented in Table 2.

In Case 1 (the example without seasonal dynamics in fine root biomass), estimates of both production and mortality as a percentage of the "true" value were 16.6% for Method I and 25.5% for Method II. In this case, both methods derived these estimates of production and

mortality from apparent seasonal dynamics which were merely the result of sampling error. These values compare with zero values in the deterministic simulation.

In Case 2, the introduction of sampling error (±10%) affected the means of the rates only slightly (<0.6%), although the error ranged up to 17.2%. Increasing the sampling error to ±30% affected the means slightly more (<1.2%) and raised the maximum error for an individual run to 22.0%.

In Cases 3 and 4, the mean estimates of production and mortality were increased slightly (a maximum increase of 2.7%) by the introduction of sampling error. However, individual runs differed by up to 16.1% from the run without sampling error.

DISCUSSION

The estimates of fine root production and mortality from sequential sampling of fine root biomass include three major sources of uncertainty: 1) the possibility of concurrence of the two major processes which determine live fine root biomass (production and mortality); 2) uncertainty regarding the accuracy of the estimates of

live and dead fine root biomass; and 3) uncertainty whether the selected sampling dates coincide with the peaks and troughs in the seasonal pattern. The emphasis of this analysis was on the first two of these three sources of uncertainty.

The results demonstrate that the degree of simultaneity of input into and outflow from a system component (production and mortality, respectively, in the case of live fine roots) greatly affects the accuracy of estimates of transfer rates derived from the pattern of temporal changes in that system component. The two commonly used computational methods which were tested in this study estimated fine root production and mortality rates without systematic error only if there was a complete temporal separation in the occurrence of the two rates in the model (as in Case 2).

Any temporal overlap in the action of the rate variables will cause underestimation of production and mortality rates. The error becomes greater with increasing temporal overlap of the two processes because the difference between net and gross transfers increases (cf. Cases 3 and 4). Case 1 is an extreme example for which the standard methods of computing production and mortality are inadequate.

The four cases presented here are merely examples which cover the theoretical range of temporal separation of fine root production and mortality. Other seasonal patterns and turnover rates can be generated by selecting different values for the rate variables. In general, the degree of systematic underestimation of annual production and mortality is proportional to the length of the periods of their simultaneous occurrence, as well as their relative size in any time step (or sampling interval).

A comparison of the results obtained from the two computational methods showed no difference in Cases 1 and 2, and a slight superiority of Method II in Cases 3 and 4. However, relative to the size of the systematic error due to the concurrence of processes, the improvement in the estimates obtained by Method II is fairly small. Neither Method I nor the more elaborate Method II overcame this systematic error.

Introducing random errors to the measurements of fine root biomass did not alter the general conclusions reached above. For examples other than Case 1, the mean estimates of production and mortality did not change, or changed very little, when compared with the estimates obtained from runs without sampling error. However, for

individual runs, the ±10% sampling error affected the accuracy of the production estimates by up to 17%. Assessed independently of the systematic error discussed above, this sampling error led to either under- or overestimation of production and mortality rates. Overestimation is more likely to occur in a system with little seasonal dynamics in fine root biomass, small turnover rates and large sampling errors. Conversely, in a system with a pronounced seasonal pattern and a temporal separation of the rates, sampling error may cause either overestimation or underestimation of production and mortality rates, as in Case 2. There was no evidence that subtracting a correction factor to account for overestimation of production rates as suggested by Persson (1978) would improve the accuracy of the estimates. Such a correction would increase the error in many of the runs of all four cases.

The timing of sampling dates to coincide with peaks and troughs of fine root biomass is important (Vogt et al. 1986a). Missing the peaks or troughs will yield production and mortality estimates which are smaller than the true values.

CONCLUSIONS

Two of the three major sources of uncertainty associated with fine root production and mortality estimates obtained from seasonal data on fine root biomass potentially can cause an underestimate of the true turnover rates. The remaining source of uncertainty may cause either overestimation or underestimation.

Future research should attempt to obtain more direct measures of production and mortality rates (e.g. by including fine root decomposition experiments in production studies). The physiology of fine roots, including fine root longevity and factors which cause fine root mortality, should also receive more research attention.

ACKNOWLEDGEMENTS

Financial support received from the Canadian Forestry Service and WAK's personal funding from a World University of Canada Scholarship are gratefully acknowledged. We thank Ann McGee and Phil Comeau for helpful comments on the manuscript. The comments of Kristiina Vogt and one anonymous reviewer were appreciated.

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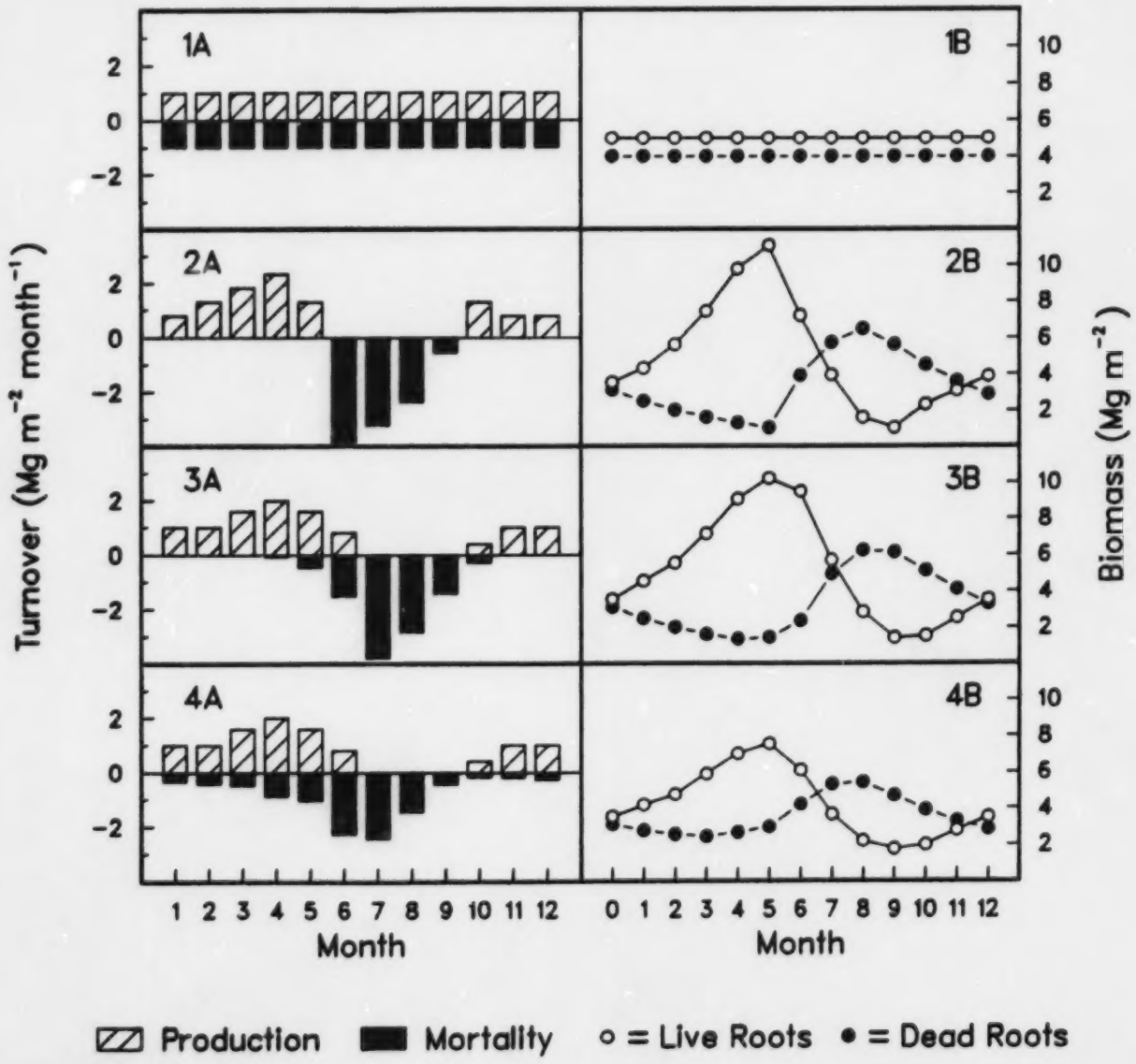
TABLE 1: Estimates of annual production and mortality rates expressed as a percentage of the "true" (i.e. simulated) values. See text for explanation of the cases and computational methods.

	CASE			
	1	2	3	4
	---------- (%) ----------			
METHOD I				
Production	0.0	100.0	84.5	55.4
Mortality	0.0	100.0	84.5	55.4
METHOD II				
Production	0.0	100.0	87.4	60.6
Mortality	0.0	100.0	87.4	60.6

TABLE 2: Estimates of production and mortality expressed as a percentage of the "true" (i.e. simulated) values. Mean, standard deviation, minimum and maximum obtained from a Monte Carlo simulation with 1000 runs for each of the four cases. See text for explanation of the cases and computational methods.

	CASE 1	2	3	4
METHOD I				
Production				
Mean	16.6	100.2	85.6	56.1
St. Dev.	4.2	6.5	5.5	4.7
Minimum	3.7	84.1	71.4	42.9
Maximum	31.0	116.7	99.0	70.9
Mortality				
Mean	16.6	100.1	85.6	56.2
St. Dev.	4.2	6.1	4.8	3.8
Minimum	4.5	88.4	73.7	46.8
Maximum	31.7	111.8	95.3	65.8
METHOD II				
Production				
Mean	25.5	100.6	90.2	63.2
St. Dev.	5.0	6.1	5.3	4.7
Minimum	9.6	84.1	76.2	49.8
Maximum	45.4	117.2	103.3	76.4
Mortality				
Mean	25.5	100.5	90.3	63.2
St. Dev.	4.8	5.7	4.5	3.9
Minimum	12.6	88.5	77.8	53.1
Maximum	46.8	112.4	100.9	72.4

FIGURE 1: Monthly production and mortality rates of fine roots and the resulting patterns in live and dead fine root biomasses for Cases 1 through 4.


1A
1B
2A
2B
3A
3B
4A
4B
Turnover (Mg m^{-2} month^{-1})
Biomass (Mg m^{-2})
Month
Month
Production
Mortality
o = Live Roots
• = Dead Roots

APPENDIX 2

Mean, (standard error), and sample size (n) for ash content, expressed as percentage of sample dry weight for each installation and soil layer. Installation 99 refers to the mean of the 5 Installations. Horizon 4 refers to the mean of the 3 horizons. Data are based on a total of 2225 samples.

MEAN AND STANDARD ERROR (...) OF PERCENT ASH CONTENT. 20. 3.1987 11:21:38

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF - 50 cm

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	7.18	43.89	5.23	4.55	6.01	13.61	48.47	5.75	8.37		10.44	56.11	29.88
	(1.09)	(15.53)	(1.40)	(1.37)	(2.36)	(2.00)	(29.64)	(4.08)	(5.28)	( )	(3.75)	(8.92)	(8.91)
5	8.55	35.23	4.38	3.01		14.25	37.67				10.33	43.98	37.36
	(1.76)	(12.49)	(2.58)	(3.07)	( )	(5.18)	(12.18)	( )	( )	( )	(3.05)	(17.49)	(4.46)
16	11.09	44.16	10.61	3.43		16.13	51.10				23.71	64.15	33.91
	(2.00)	(7.90)	(4.84)	(4.31)	( )	(4.80)	(12.26)	( )	( )	( )	(14.07)	(7.73)	(29.88)
71	14.50	49.66	5.92	7.70	8.22	20.38	59.39	4.96	14.58		20.00	65.46	47.43
	(3.08)	(18.49)	(1.48)	(9.31)	( )	(2.84)	(21.39)	( )	( )	( )	(8.05)	(5.16)	(18.13)
72	9.92	52.56	3.28	2.58		13.49	50.38				13.62	38.68	31.52
	(4.71)	(26.69)	(3.60)	( )	( )	(6.73)	(32.35)	( )	( )	( )	(3.22)	(27.88)	(8.39)
99	10.30	44.39	6.45	4.28	6.75	15.92	49.31	5.61	9.61		14.97	57.15	35.25
	(1.14)	(5.17)	(1.45)	(1.10)	(3.17)	(1.71)	(6.43)	(3.10)	(4.97)	( )	(2.95)	(4.83)	(5.16)

NUMBER OF SAMPLES IN EACH CLASS

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	23	5	17	6	2	22	3	5	4		11	12	5
5	20	7	6	4		11	5				11	10	3
16	25	12	12	2		19	4				10	16	3
71	22	7	8	2	1	20	5	1	1		7	15	6
72	14	4	4	1		10	3				16	5	13
99	104	35	47	15	3	82	20	6	5		55	58	30

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MEAN AND STANDARD ERROR (...) OF PERCENT ASH CONTENT.

HORIZON : 2 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF - 50 cm

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	12.30	39.82	9.06	10.07	11.39	20.16	48.69	15.15	16.91	8.54	16.82	68.33	43.34
	(0.91)	(3.27)	(1.41)	(3.00)	(10.38)	(1.50)	(5.67)	(3.71)	(5.62)	(36.68)	(4.21)	(4.31)	(8.24)
5	13.51	37.80	7.79	11.37	4.94	16.88	46.63	8.39	10.84	14.71	15.45	51.25	30.26
	(2.86)	(6.73)	(2.21)	(5.42)	( )	(1.82)	(6.85)	(2.52)	(2.11)	(74.78)	(4.30)	(8.84)	(83.42)
16	15.26	52.63	10.31	10.31	15.37	28.52	62.14	17.08	10.80		27.55	73.26	57.31
	(1.82)	(4.11)	(1.92)	(5.05)	(13.97)	(5.75)	(4.45)	(7.47)	(9.84)	( )	(11.38)	(7.01)	(29.61)
71	15.14	47.42	11.52	10.64	8.25	20.64	54.57	15.53	18.53	5.94	22.22	67.89	34.88
	(1.70)	(4.51)	(3.75)	(3.18)	(7.17)	(2.61)	(5.85)	(6.76)	(5.44)	(11.98)	(5.28)	(10.07)	(3.14)
72	17.46	45.14	10.29	10.41	8.86	19.70	52.63	11.12	8.64		23.98	61.12	44.87
	(4.23)	(7.85)	(2.79)	(4.39)	( )	(2.97)	(13.89)	(4.21)	(4.53)	( )	(5.60)	(7.81)	(7.99)
99	14.49	44.74	9.83	10.51	10.99	21.16	53.54	14.22	14.65	9.73	20.92	64.51	42.40
	(1.00)	(2.38)	(1.09)	(1.61)	(3.82)	(1.55)	(2.88)	(2.49)	(2.49)	(6.10)	(2.69)	(3.86)	(4.20)

NUMBER OF SAMPLES IN EACH CLASS

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	26	22	20	18	4	22	15	15	12	2	22	9	11
5	24	19	17	10	1	21	16	8	8	2	14	11	2
16	23	23	20	11	4	20	20	10	4		14	12	4
71	24	20	20	15	4	22	16	15	11	2	22	9	10
72	16	12	14	5	1	16	6	5	4		15	7	12
99	113	96	91	59	14	101	73	53	39	6	87	48	39

MEAN AND STANDARD ERROR (...) OF PERCENT ASH CONTENT. 20. 3.1987 11:21:38

HORIZON : 3 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF - 50 cm

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	14.28	44.48	10.77	13.57	11.79	19.07	51.68	15.04	21.69	32.52	20.92	68.15	33.92
	(1.64)	(7.14)	(1.98)	(4.08)	(12.59)	(1.68)	(7.85)	(4.52)	(7.95)	(34.18)	(7.16)	(113.35)	(3.91)
5	15.61	32.13	12.60	7.95		17.42	42.63	15.05	24.44		11.00	47.40	25.04
	(4.06)	(10.31)	(4.47)	(40.94)	( )	(2.83)	(8.51)	(13.45)	(11.46)	( )	(1.98)	(22.16)	(8.51)
16	16.04	47.47	14.17	13.79	28.97	23.95	55.25	23.04	18.75		17.09	59.30	40.04
	(2.21)	(4.77)	(3.90)	(5.05)	(6.41)	(4.58)	(6.31)	(13.48)	( )	( )	(13.73)	(199.49)	(13.99)
71	23.02	41.61	14.63	12.07	16.44	26.47	56.98	17.86	18.38	17.20	18.01	70.96	35.21
	(4.67)	(7.80)	(3.88)	(3.20)	(24.09)	(4.04)	(6.79)	(2.84)	(14.01)	( )	(3.29)	( )	(4.99)
72	17.63	46.74	10.21	11.39	11.64	22.24	55.38	12.05	31.48		24.13	78.51	35.89
	(4.70)	(14.46)	(2.54)	(4.56)	( )	(5.68)	(25.07)	(40.23)	(138.17)	( )	(27.39)	(33.66)	(8.62)
99	17.11	43.56	12.66	12.68	16.61	22.07	53.29	17.17	21.99	27.41	17.33	64.19	35.01
	(1.56)	(3.29)	(1.49)	(1.85)	(6.75)	(1.75)	(3.41)	(2.79)	(5.18)	(22.79)	(2.53)	(11.44)	(2.86)

NUMBER OF SAMPLES IN EACH CLASS

INST. CODE	CLO	CLOC	CL1	CL2	CL3	CDO	CDOC	CD1	CD2	CD3	NC	M	R
2	22	18	13	13	4	21	11	11	5	2	11	2	16
5	21	8	12	2		16	6	4	3		11	2	3
16	22	19	13	10	2	23	13	6	1		5	2	7
71	19	11	14	11	3	21	13	10	6	1	16	1	15
72	10	7	9	5	1	11	4	2	2		3	2	10
99	84	63	61	41	10	92	47	33	17	3	46	9	51

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MEAN AND STANDARD ERROR (...) OF PERCENT ASH CONTENT.

HORIZON : 4 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF - 50 cm

INST. CODE	CL0	CL0C	CL1	CL2	CL3	CD0	CD0C	CD1	CD2	CD3	NC	M	R
2	11.25	42.13	8.20	10.40	10.47	17.59	49.80	13.59	16.42	20.53	16.25	61.94	36.53
	(0.97)(	3.36)(	1.05)(	2.16)(	4.56)(	1.19)(	4.06)(	2.59)(	3.89)(	22.59)(	2.92)(	5.40)(	3.75)
5	12.66	35.93	8.85	6.85	4.94	16.46	44.08	10.61	14.55	14.71	12.53	47.76	30.96
	(1.82)(	4.65)(	2.02)(	3.77)(	)(	1.59)(	4.60)(	3.82)(	4.71)(	74.78)(	1.99)(	7.93)(	5.88)
16	14.01	48.93	11.51	11.22	19.90	23.03	58.53	19.32	12.39		24.42	67.47	43.66
	(1.22)(	2.92)(	1.81)(	3.21)(	10.27)(	3.02)(	3.44)(	6.06)(	7.99)(	)(	6.98)(	5.24)(	9.91)
71	17.23	46.15	11.49	10.99	11.31	22.50	56.20	16.02	18.26	9.69	20.38	66.56	37.47
	(1.95)(	4.14)(	2.29)(	2.01)(	6.14)(	1.89)(	4.12)(	3.95)(	4.76)(	16.20)(	2.92)(	4.33)(	3.99)
72	14.86	46.92	9.23	10.14	10.25	18.78	52.96	11.39	16.25		19.12	55.59	37.35
	(2.67)(	5.94)(	1.86)(	2.76)(	17.63)(	2.72)(	7.82)(	3.10)(	14.52)(	)(	3.40)(	11.50)(	4.75)
99	13.88	44.29	9.90	10.47	12.60	19.90	52.85	14.72	16.28	15.62	18.30	60.77	37.47
	(0.76)(	1.81)(	0.81)(	1.15)(	3.18)(	1.00)(	2.06)(	1.81)(	2.29)(	8.44)(	1.65)(	3.04)(	2.25)

NUMBER OF SAMPLES IN EACH CLASS

INST. CODE	CL0	CL0C	CL1	CL2	CL3	CD0	CD0C	CD1	CD2	CD3	NC	M	R
2	71	45	50	37	10	65	29	31	21	4	44	23	32
5	65	34	35	16	1	48	27	12	11	2	36	23	8
16	70	54	45	23	6	62	37	16	5		29	30	14
71	65	38	42	28	8	63	34	26	18	3	45	25	31
72	40	23	27	11	2	37	13	7	6		34	14	35
99	311	194	199	115	27	275	140	92	61	9	188	115	120

APPENDIX 3

Mean, (standard error), and sample size (n) of ash-free root dry weight for each root class, horizon, Installation and sampling date. Note that sampling dates 5 and 7 have not been processed. Only Installation 72 was processed for the 6. sampling date.

1. SAMPLING PERIOD
MEAN AND STANDARD ERROR (...) OF ASH FREE ROOT WEIGHT [g/m2] (DIVIDE BY 100 TO OBTAIN Mg/ha)

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF + A, 5 = A + B, 6 = FF + A + B

CODE / INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	17	179.62	32.72	35.56	0.0	39.99	6.82	11.46	0.0	50.43	37.24	1877.54	212.34	46.81
		(31.00)(	9.62)(	15.07)(	0.0)(	5.58)(	3.57)(	7.19)(	0.0)(	18.22)(	7.95)(	272.28)(	24.86)(	7.70)
5	16	76.46	11.19	9.53	0.0	17.97	0.90	0.08	0.0	15.35	46.42	973.84	87.65	18.86
		(19.21)(	6.52)(	7.46)(	0.0)(	6.49)(	0.82)(	0.08)(	0.0)(	2.96)(	10.49)(	276.67)(	24.83)(	6.61)
16	17	85.22	12.42	12.74	0.0	31.05	0.51	0.0	0.0	19.18	61.95	1622.51	97.64	31.56
		(15.27)(	3.95)(	8.60)(	0.0)(	6.06)(	0.35)(	0.0)(	0.0)(	8.07)(	21.71)(	365.17)(	17.51)(	6.05)
71	15	53.60	9.85	19.48	10.18	23.20	0.93	2.91	0.0	12.33	65.88	531.50	63.45	24.13
		(13.19)(	4.52)(	19.48)(	10.18)(	3.30)(	0.62)(	2.63)(	0.0)(	2.38)(	22.40)(	78.05)(	16.70)(	3.21)
72	17	15.57	8.01	8.59	0.0	14.13	0.0	0.0	0.0	34.74	14.94	1425.68	23.58	14.13
		(5.10)(	7.06)(	8.59)(	0.0)(	5.12)(	0.0)(	0.0)(	0.0)(	8.24)(	9.03)(	401.08)(	11.67)(	5.12)

HORIZON : 2

CODE / INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	17	301.26	135.37	216.85	64.15	112.45	20.11	91.99	57.40	304.16	19.43	1464.36	436.63	132.56
		(31.70)(	19.40)(	45.48)(	43.93)(	25.47)(	3.91)(	19.64)(	50.26)(	120.63)(	5.35)(	163.25)(	44.13)(	24.72)
5	16	101.29	59.06	85.98	26.35	44.66	7.62	65.25	0.0	34.62	19.96	800.12	160.35	52.27
		(15.15)(	11.84)(	31.47)(	26.35)(	6.07)(	2.94)(	36.38)(	0.0)(	6.79)(	7.43)(	115.89)(	24.53)(	8.06)
16	17	159.44	68.70	143.72	158.02	73.06	10.04	32.97	0.0	23.66	14.53	882.65	228.14	83.10
		(21.13)(	12.70)(	65.56)(	83.90)(	10.45)(	3.71)(	13.72)(	0.0)(	6.32)(	4.38)(	101.30)(	31.16)(	12.32)
71	15	161.21	82.33	139.84	38.03	75.61	26.29	67.59	0.0	115.97	10.02	1036.28	243.54	101.90
		(32.88)(	19.66)(	38.93)(	27.59)(	9.81)(	5.50)(	31.30)(	0.0)(	51.01)(	3.15)(	180.83)(	49.06)(	12.39)
72	17	67.35	42.56	22.69	0.0	53.12	7.20	1.55	2.45	59.33	17.91	894.21	109.91	60.32
		(8.42)(	8.58)(	11.03)(	0.0)(	7.58)(	2.79)(	1.26)(	2.45)(	13.37)(	8.95)(	108.36)(	12.85)(	8.12)

HORIZON : 3

CODE / INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	17	94.02	48.50	157.53	217.70	52.24	16.53	10.01	0.0	25.52	1.00	503.38	142.52	68.78
		(13.13)(	12.80)(	78.96)(	136.88)(	9.45)(	5.42)(	4.21)(	0.0)(	8.04)(	0.42)(	72.66)(	33.18)(	11.83)
5	16	34.13	29.05	12.84	0.0	14.78	1.27	0.84	9.43	18.95	1.14	411.62	63.18	16.05
		(6.83)(	8.14)(	10.27)(	0.0)(	3.81)(	0.62)(	0.84)(	9.43)(	5.96)(	0.62)(	77.19)(	12.83)(	3.96)
16	17	73.58	33.11	69.66	14.96	27.97	7.67	12.60	0.0	7.28	1.46	336.75	106.69	35.63
		(12.56)(	9.43)(	36.75)(	14.96)(	4.37)(	2.69)(	7.62)(	0.0)(	2.01)(	0.53)(	58.48)(	30.04)(	5.54)
71	15	49.15	48.81	79.88	101.93	32.25	18.36	48.77	0.0	62.39	1.32	382.88	87.96	50.61
		(13.09)(	12.66)(	25.56)(	58.84)(	6.41)(	5.27)(	31.15)(	0.0)(	34.84)(	1.11)(	66.11)(	23.90)(	8.21)
72	17	27.84	20.66	28.40	0.0	10.99	4.49	0.26	0.0	9.75	1.01	380.16	48.51	15.48
		(10.37)(	6.30)(	15.57)(	0.0)(	3.32)(	1.90)(	0.26)(	0.0)(	3.23)(	0.32)(	57.38)(	14.84)(	4.98)

2. SAMPLING PERIOD
MEAN AND STANDARD ERROR (...) OF ASH FREE ROOT WEIGHT [g/m2] (DIVIDE BY 100 TO OBTAIN Mg/ha)

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF + A, 5 = A + B, 6 = FF + A + B

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
INST.	N													
2	10	240.24	67.13	25.04	90.63	49.63	2.56	5.79	0.0	58.94	55.67	1871.85	307.37	52.18
		(23.76)	(13.70)	(17.40)	(72.64)	(11.46)	(1.44)	(3.92)	(0.0)	(30.37)	(22.98)	(286.65)	(28.90)	(12.18)
5	11	58.16	4.82	7.61	0.0	7.12	0.79	0.0	0.0	16.08	20.44	714.45	62.97	7.92
		(6.85)	(2.02)	(5.29)	(0.0)	(1.89)	(0.53)	(0.0)	(0.0)	(5.94)	(5.53)	(65.88)	(7.64)	(1.83)
16	10	71.88	7.72	7.11	0.0	13.96	0.0	0.0	0.0	43.33	76.56	1084.06	79.60	13.96
		(11.65)	(4.58)	(7.11)	(0.0)	(4.47)	(0.0)	(0.0)	(0.0)	(36.70)	(21.92)	(197.91)	(14.16)	(4.47)
71	10	56.42	6.52	0.0	0.0	35.35	0.87	0.0	0.0	17.97	54.44	450.72	62.94	36.22
		(15.39)	(4.45)	(0.0)	(0.0)	(8.42)	(0.87)	(0.0)	(0.0)	(3.99)	(20.96)	(59.54)	(19.50)	(8.27)
72	10	19.20	4.03	0.0	0.0	16.04	1.31	0.0	0.0	28.14	3.73	665.04	23.23	17.34
		(5.99)	(2.71)	(0.0)	(0.0)	(6.03)	(0.93)	(0.0)	(0.0)	(11.98)	(2.17)	(154.55)	(8.32)	(5.84)

HORIZON : 2

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
INST.	N													
2	10	260.79	137.93	177.78	47.78	61.25	12.91	28.85	0.0	202.04	10.65	1287.28	398.72	74.16
		(39.85)	(17.73)	(50.03)	(25.46)	(8.89)	(3.37)	(11.57)	(0.0)	(54.23)	(5.64)	(176.32)	(55.62)	(11.18)
5	11	111.64	33.62	33.31	0.0	61.31	11.39	13.82	58.15	24.30	15.71	1750.44	145.26	72.71
		(19.06)	(9.93)	(13.69)	(0.0)	(10.59)	(3.66)	(7.91)	(47.61)	(7.23)	(7.49)	(231.50)	(27.36)	(13.81)
16	10	139.66	73.62	59.03	89.28	37.12	10.66	7.17	0.0	54.10	22.66	900.37	213.29	47.78
		(32.00)	(14.10)	(22.93)	(39.76)	(7.21)	(3.27)	(7.17)	(0.0)	(41.28)	(9.98)	(102.61)	(42.20)	(9.16)
71	10	151.52	42.53	103.86	51.91	149.90	28.92	42.59	58.81	297.61	11.47	1320.72	194.05	178.81
		(30.38)	(19.71)	(35.62)	(34.81)	(24.80)	(10.40)	(27.00)	(58.81)	(130.81)	(4.72)	(155.21)	(43.59)	(31.28)
72	10	49.96	17.32	16.97	19.37	39.44	8.30	16.04	0.0	75.36	4.69	972.68	67.28	47.74
		(13.00)	(6.65)	(8.78)	(19.37)	(8.86)	(4.57)	(6.83)	(0.0)	(33.83)	(1.41)	(192.52)	(18.36)	(10.37)

HORIZON : 3

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
INST.	N													
2	10	74.57	41.69	29.84	44.66	36.27	12.82	5.71	45.19	45.28	0.99	620.54	116.26	49.09
		(18.53)	(11.91)	(15.15)	(23.71)	(11.38)	(7.25)	(3.39)	(30.81)	(22.50)	(0.51)	(199.90)	(29.64)	(15.02)
5	11	41.78	14.55	6.34	0.0	22.90	5.54	7.37	0.0	187.69	1.67	1104.64	56.33	28.45
		(9.53)	(8.14)	(6.34)	(0.0)	(3.85)	(2.64)	(7.03)	(0.0)	(134.11)	(1.06)	(105.91)	(14.22)	(4.18)
16	10	74.81	44.14	87.23	97.51	38.17	6.35	7.88	0.0	3.49	4.20	857.52	118.95	44.52
		(15.26)	(10.89)	(38.85)	(71.11)	(8.19)	(2.38)	(7.88)	(0.0)	(1.22)	(2.17)	(81.33)	(24.90)	(9.97)
71	10	77.28	15.42	58.04	13.60	61.82	13.69	23.18	10.33	44.84	1.23	995.32	92.71	75.50
		(13.87)	(4.95)	(18.94)	(13.60)	(17.25)	(3.89)	(13.12)	(10.33)	(7.78)	(0.47)	(79.67)	(17.49)	(19.63)
72	10	35.23	21.50	20.52	32.65	33.38	8.19	5.26	0.0	15.11	1.27	353.31	56.73	41.56
		(10.84)	(8.52)	(12.46)	(32.65)	(12.15)	(5.42)	(3.47)	(0.0)	(9.61)	(0.73)	(68.25)	(18.90)	(12.90)

3. SAMPLING PERIOD
MEAN AND STANDARD ERROR (...) OF ASH FREE ROOT WEIGHT [g/m2] (DIVIDE BY 100 TO OBTAIN Mg/ha)

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF + A, 5 = A + B, 6 = FF + A + B

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	N	R	CL0+1	CD0+1
INST.	N													
2	10	184.41	41.59	100.97	0.0	65.02	9.58	11.43	0.0	43.44	39.34	1373.00	226.01	74.59
		(36.74)(	10.24)(	35.91)(	0.0)(	10.28)(	5.46)(	5.61)(	0.0)(	29.75)(	12.29)(	193.30)(	41.91)(	12.52)
5	10	25.70	5.30	0.0	74.09	44.07	0.44	0.0	0.0	22.78	7.25	356.49	31.00	44.51
		(10.88)(	3.53)(	0.0)(	74.09)(	16.22)(	0.44)(	0.0)(	0.0)(	8.93)(	3.15)(	80.41)(	12.32)(	16.61)
16	10	49.35	3.72	0.0	0.0	16.98	0.0	0.0	0.0	5.29	20.04	387.10	53.06	16.98
		(18.12)(	2.92)(	0.0)(	0.0)(	5.71)(	0.0)(	0.0)(	0.0)(	1.84)(	8.57)(	99.37)(	20.47)(	5.71)
71	10	12.87	1.30	0.0	0.0	91.79	1.74	0.0	0.0	25.50	14.04	242.35	14.18	93.53
		(5.94)(	0.93)(	0.0)(	0.0)(	16.74)(	1.33)(	0.0)(	0.0)(	6.34)(	9.89)(	26.95)(	5.76)(	17.53)
72	10	0.0	0.0	0.0	0.0	30.32	11.34	6.26	3.51	33.52	2.55	304.65	0.0	41.65
		(0.0)(	0.0)(	0.0)(	0.0)(	10.11)(	7.56)(	6.26)(	3.51)(	13.44)(	1.15)(	86.50)(	0.0)(	14.91)

HORIZON : 2

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	N	R	CL0+1	CD0+1
INST.	N													
2	10	180.20	94.37	112.83	0.0	108.66	27.07	9.29	74.09	959.69	9.51	1539.79	274.56	135.73
		(24.11)(	23.07)(	34.38)(	0.0)(	23.28)(	8.54)(	4.56)(	74.09)(	413.91)(	5.54)(	207.21)(	42.68)(	24.93)
5	10	47.31	24.28	13.10	0.0	104.66	11.00	24.71	0.0	38.28	4.05	987.89	71.60	115.67
		(10.25)(	9.29)(	6.85)(	0.0)(	18.46)(	3.80)(	13.11)(	0.0)(	8.17)(	1.33)(	103.19)(	16.33)(	16.80)
16	10	120.58	52.20	63.81	118.45	63.58	11.87	28.84	0.0	16.07	37.56	1257.28	172.78	75.45
		(22.18)(	14.45)(	23.15)(	95.29)(	7.47)(	5.28)(	26.21)(	0.0)(	6.31)(	14.45)(	186.83)(	31.84)(	9.46)
71	10	46.02	48.23	29.31	154.28	264.71	26.14	16.56	116.34	384.46	8.60	1121.37	94.25	290.85
		(10.15)(	15.72)(	18.73)(	90.81)(	32.59)(	6.86)(	13.14)(	116.34)(	244.04)(	2.73)(	97.31)(	20.85)(	33.28)
72	10	0.38	1.66	8.28	137.75	132.52	23.81	26.17	4.17	42.14	7.01	846.75	2.04	156.34
		(0.38)(	1.11)(	7.83)(	137.75)(	13.46)(	7.69)(	7.20)(	4.17)(	10.96)(	2.22)(	103.54)(	1.39)(	18.11)

HORIZON : 3

CODE		CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	N	R	CL0+1	CD0+1
INST.	N													
2	10	63.83	34.87	78.57	0.0	76.23	37.70	3.26	0.0	54.84	10.08	1136.71	118.70	113.93
		(13.55)(	11.17)(	33.39)(	0.0)(	13.53)(	6.72)(	3.26)(	0.0)(	27.52)(	9.35)(	178.90)(	20.63)(	17.55)
5	10	14.67	3.23	6.86	0.0	51.26	9.03	19.55	0.0	16.86	0.66	733.77	17.90	60.29
		(4.13)(	1.68)(	4.58)(	0.0)(	10.43)(	4.38)(	14.35)(	0.0)(	5.43)(	0.27)(	62.69)(	4.68)(	10.98)
16	10	65.33	19.82	32.57	37.37	60.95	15.64	6.13	0.0	4.98	4.47	647.27	85.16	76.59
		(15.10)(	8.90)(	24.64)(	37.37)(	10.36)(	5.74)(	3.80)(	0.0)(	1.28)(	2.78)(	92.55)(	23.01)(	15.00)
71	10	24.69	9.07	20.31	11.58	121.88	14.42	27.52	16.77	139.76	1.82	887.92	33.77	136.30
		(5.42)(	3.67)(	10.96)(	11.58)(	19.10)(	4.69)(	12.42)(	13.19)(	56.31)(	1.22)(	99.95)(	8.20)(	20.22)
72	10	1.52	0.41	21.29	88.89	54.80	24.49	20.90	0.0	87.27	23.49	541.63	1.94	79.39
		(1.16)(	0.41)(	14.87)(	61.54)(	7.78)(	6.80)(	14.08)(	0.0)(	68.09)(	23.31)(	69.31)(	1.18)(	13.12)

4. SAMPLING PERIOD
MEAN AND STANDARD ERROR (...) OF ASH FREE ROOT WEIGHT [g/m2] (DIVIDE BY 100 TO OBTAIN Mg/ha)

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF + A, 5 = A + B, 6 = FF + A + B

CODE INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	10	41.59	16.64	6.17	0.0	145.31	3.05	0.0	0.0	36.41	3.65	550.96	58.23	148.36
		(10.27)	(6.55)	(6.17)	(0.0)	(24.63)	(1.46)	(0.0)	(0.0)	(17.39)	(2.02)	(77.03)	(12.17)	(24.26)
5	10	21.97	15.90	10.75	0.0	48.14	2.18	0.84	0.0	14.91	9.32	453.72	37.87	50.32
		(11.86)	(13.97)	(8.56)	(0.0)	(14.66)	(1.17)	(0.84)	(0.0)	(5.50)	(7.92)	(108.31)	(25.35)	(14.72)
16	10	9.04	2.06	9.73	0.0	90.72	3.92	3.76	0.0	26.78	12.75	536.08	11.10	94.65
		(3.66)	(1.11)	(9.73)	(0.0)	(26.50)	(2.64)	(3.76)	(0.0)	(15.85)	(5.00)	(157.64)	(3.83)	(27.08)
71	10	10.11	3.04	0.0	0.0	74.47	4.80	0.42	0.0	25.13	5.26	274.89	13.15	79.26
		(4.75)	(1.59)	(0.0)	(0.0)	(15.60)	(2.29)	(0.42)	(0.0)	(8.76)	(1.81)	(56.29)	(4.49)	(16.40)
72	10	0.0	0.0	0.0	0.0	40.94	3.49	0.0	0.0	95.76	1.42	478.96	0.0	44.42
		(0.0)	(0.0)	(0.0)	(0.0)	(13.65)	(2.03)	(0.0)	(0.0)	(34.54)	(1.42)	(152.81)	(0.0)	(15.00)

HORIZON : 2

CODE INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	10	100.16	97.05	209.38	142.04	304.54	32.53	38.77	5.00	155.62	4.83	1085.98	197.21	337.07
		(22.91)	(28.02)	(45.17)	(52.09)	(47.47)	(11.63)	(16.97)	(5.00)	(85.45)	(2.78)	(108.96)	(48.04)	(53.23)
5	10	16.27	16.19	25.39	0.0	84.20	16.08	24.71	288.98	16.79	5.18	1051.21	32.46	100.29
		(4.11)	(6.53)	(11.23)	(0.0)	(19.04)	(4.75)	(22.06)	(188.07)	(4.44)	(3.15)	(311.73)	(9.51)	(20.47)
16	10	41.50	29.00	38.12	64.50	180.82	19.15	7.01	40.03	39.16	10.25	676.17	70.50	199.97
		(9.57)	(7.28)	(21.14)	(43.08)	(31.19)	(4.12)	(4.99)	(40.03)	(9.02)	(5.84)	(105.92)	(15.70)	(32.17)
71	10	33.90	31.06	45.41	8.05	240.00	47.21	54.95	2.92	259.06	4.60	1013.69	64.96	287.22
		(10.59)	(10.25)	(18.18)	(8.05)	(42.81)	(14.52)	(13.84)	(2.92)	(87.48)	(2.21)	(118.94)	(20.27)	(49.90)
72	10	1.14	0.0	7.45	0.0	138.96	35.31	71.33	0.0	111.32	3.23	972.81	1.14	174.27
		(0.81)	(0.0)	(7.45)	(0.0)	(23.91)	(7.17)	(30.55)	(0.0)	(47.01)	(1.60)	(177.67)	(0.81)	(27.66)

HORIZON : 3

CODE INST.	N	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	10	47.24	32.56	69.07	41.16	114.67	10.60	11.58	0.0	50.78	0.0	785.36	79.80	125.27
		(9.78)	(9.82)	(23.47)	(41.16)	(21.68)	(3.84)	(5.83)	(0.0)	(14.20)	(0.0)	(68.96)	(15.66)	(22.02)
5	10	15.59	10.50	6.05	0.0	44.58	15.30	18.85	80.14	11.10	0.0	919.04	26.09	59.89
		(3.58)	(7.05)	(4.30)	(0.0)	(7.69)	(9.15)	(13.60)	(80.14)	(3.30)	(0.0)	(171.07)	(8.59)	(10.97)
16	10	25.07	15.07	11.55	9.25	91.45	17.06	18.74	9.72	48.26	0.83	687.15	40.13	108.51
		(10.18)	(7.45)	(11.55)	(9.25)	(32.89)	(6.29)	(11.23)	(9.72)	(15.29)	(0.51)	(103.77)	(16.99)	(26.07)
71	10	15.47	14.99	20.31	282.56	124.27	33.01	12.07	57.01	358.67	0.0	746.47	30.46	157.29
		(4.35)	(7.03)	(13.76)	(210.53)	(22.63)	(8.94)	(10.44)	(57.01)	(178.58)	(0.0)	(70.42)	(10.19)	(27.34)
72	10	3.42	3.32	0.0	0.0	44.15	26.79	76.40	136.48	37.15	0.66	788.91	6.74	70.94
		(2.08)	(3.32)	(0.0)	(0.0)	(11.30)	(8.48)	(31.83)	(82.99)	(18.44)	(0.44)	(89.66)	(3.58)	(17.41)

6. SAMPLING PERIOD
MEAN AND STANDARD ERROR (...) OF ASH FREE ROOT WEIGHT [g/m2] (DIVIDE BY 100 TO OBTAIN Mg/ha)

HORIZON : 1 1 = FF, 2 = A (0 - 30 cm), 3 = B (30 - 50 cm), 4 = FF + A, 5 = A + B, 6 = FF + A + B

INST.	N	CODE	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
5	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
16	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
71	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
72	10		7.07	4.47	7.07	6.89	64.80	0.87	0.0	0.0	52.67	5.95	1030.99	11.54	65.67
		(	3.83)(	3.26)(	7.07)(	6.89)(	20.93)(	0.87)(	0.0)(	0.0)(	17.44)(	3.36)(	269.70)(	6.62)(	21.70)

HORIZON : 2

INST.	N	CODE	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
5	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
16	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
71	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
72	10		16.14	17.82	19.33	16.86	78.77	13.96	2.11	0.0	49.87	3.23	984.78	33.95	92.73
		(	7.86)(	5.46)(	8.89)(	16.86)(	19.22)(	5.62)(	2.11)(	0.0)(	16.60)(	1.69)(	413.85)(	11.56)(	22.28)

HORIZON : 3

INST.	N	CODE	CL0	CL1	CL2	CL3	CD0	CD1	CD2	CD3	NC	M	R	CL0+1	CD0+1
2	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
5	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
16	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
71	0		-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0
		(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)(	0.0)
72	10		4.18	2.90	12.28	37.75	36.20	14.82	5.77	0.0	125.83	1.82	470.27	7.09	51.13
		(	2.63)(	2.48)(	10.88)(	25.33)(	9.68)(	6.39)(	3.88)(	0.0)(	75.85)(	1.64)(	72.12)(	3.81)(	14.15)

APPENDIX 4

Example of the output file from the program which calculates production and mortality estimates for each of the five root diameter classes for each sampling interval. The complete output for all three computational methods is 90 pages long.

ALL CHANGES

INSTALLATION: 2 HORIZON: 1

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	95.03	0.0	0.0	-0.0	-0.0	-0.0	198.56		293.59
0-1	60.62	0.0	0.0	-0.0	-0.0	-0.0	155.66		216.28
1-2	34.41	0.0	0.0	-0.0	-0.0	-0.0	42.90		77.31
2-5	0.0	75.93	0.0	-0.0	-0.0	-0.0	55.12		131.05

MORTALITY: (Calculated from decreases in live root biomass)

0-2	0.0	81.36	167.78	-0.0	-0.0	-0.0	0.0	249.14
0-1	0.0	55.83	142.82	-0.0	-0.0	-0.0	0.0	198.65
1-2	0.0	25.54	24.95	-0.0	-0.0	-0.0	0.0	50.49
2-5	10.52	0.0	94.80	-0.0	-0.0	-0.0	0.0	105.32

MORTALITY: (Calculated from increases in dead root biomass)

0-2	5.37	22.41	73.77	-0.0	-0.0	-0.0	41.06	142.61
0-1	9.64	15.39	80.29	-0.0	-0.0	-0.0	36.27	141.59
1-2	0.0	7.02	0.0	-0.0	-0.0	-0.0	4.79	11.81
2-5	0.0	5.64	-0.0	-0.0	-0.0	-0.0	0.0	5.64

INSTALLATION: 2 HORIZON: 2

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	0.0	0.0	0.0	-0.0	-0.0	-0.0	217.20		217.20
0-1	0.0	0.0	0.0	-0.0	-0.0	-0.0	166.37		166.37
1-2	2.56	0.0	2.68	-0.0	-0.0	-0.0	50.83		56.07
2-5	0.0	0.0	96.55	-0.0	-0.0	-0.0	0.0		96.55

MORTALITY: (Calculated from decreases in live root biomass)

0-2	37.91	124.16	77.35	-0.0	-0.0	-0.0	0.0	239.42
0-1	40.47	80.59	80.04	-0.0	-0.0	-0.0	0.0	201.10
1-2	0.0	43.56	0.0	-0.0	-0.0	-0.0	0.0	43.56
2-5	39.07	64.95	0.0	-0.0	-0.0	-0.0	72.29	176.31

MORTALITY: (Calculated from increases in dead root biomass)

0-2	0.0	61.57	201.34	-0.0	-0.0	-0.0	0.0	262.91
0-1	0.0	47.41	195.88	-0.0	-0.0	-0.0	0.0	243.29
1-2	0.0	14.16	5.46	-0.0	-0.0	-0.0	0.0	19.62
2-5	0.0	0.0	29.48	-0.0	-0.0	-0.0	0.0	29.48

SIGNIFICANT CHANGES
ALPHA = 0.050

INSTALLATION: 2 HORIZON: 1

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	95.03	-0.0	0.0	-0.0	-0.0	-0.0	198.56		293.59
0-1	60.62	-0.0	0.0	-0.0	-0.0	-0.0	155.66		216.28
1-2	34.41	-0.0	0.0	-0.0	-0.0	-0.0	42.90		77.31
2-5	0.0	75.93	0.0	-0.0	-0.0	-0.0	55.12		131.05

MORTALITY: (Calculated from decreases in live root biomass)

0-2	0.0	-0.0	249.14	-0.0	-0.0	-0.0	0.0	249.14
0-1	0.0	-0.0	198.65	-0.0	-0.0	-0.0	0.0	198.65
1-2	0.0	-0.0	50.49	-0.0	-0.0	-0.0	0.0	50.49
2-5	0.0	0.0	94.80	-0.0	-0.0	-0.0	0.0	94.80

MORTALITY: (Calculated from increases in dead root biomass)

0-2	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	142.61	142.61
0-1	-0.0	-0.0	-0.0	-0.0	-0.0	-0.0	141.59	141.59
1-2	0.0	0.0	0.0	-0.0	-0.0	-0.0	0.0	-0.0
2-5	0.0	0.0	-0.0	-0.0	-0.0	-0.0	0.0	-0.0

INSTALLATION: 2 HORIZON: 2

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	-0.0	-0.0	0.0	-0.0	-0.0	-0.0	217.20		217.20
0-1	-0.0	-0.0	0.0	-0.0	-0.0	-0.0	166.37		166.37
1-2	0.0	0.0	-0.0	-0.0	-0.0	-0.0	53.51		53.51
2-5	-0.0	0.0	0.0	-0.0	-0.0	-0.0	0.0		-0.0

MORTALITY: (Calculated from decreases in live root biomass)

0-2	-0.0	-0.0	239.42	-0.0	-0.0	-0.0	0.0	239.42
0-1	-0.0	-0.0	201.10	-0.0	-0.0	-0.0	0.0	201.10
1-2	0.0	0.0	-0.0	-0.0	-0.0	-0.0	0.0	0.0
2-5	-0.0	0.0	0.0	-0.0	-0.0	-0.0	0.0	-0.0

MORTALITY: (Calculated from increases in dead root biomass)

0-2	0.0	-0.0	262.91	-0.0	-0.0	-0.0	0.0	262.91
0-1	0.0	-0.0	243.29	-0.0	-0.0	-0.0	0.0	243.29
1-2	0.0	-0.0	0.0	-0.0	-0.0	-0.0	0.0	-0.0
2-5	-0.0	0.0	0.0	-0.0	-0.0	-0.0	0.0	0.0

DECISION MATRIX

INSTALLATION: 2 HORIZON: 1

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	100.40	0.0	0.0	-0.0	-0.0	-0.0	239.62		340.02
0-1	70.26	0.0	0.0	-0.0	-0.0	-0.0	191.93		262.19
1-2	34.41	0.0	0.0	-0.0	-0.0	-0.0	47.69		82.10
2-5	0.0	81.57	0.0	-0.0	-0.0	-0.0	60.62		142.19

MORTALITY:

0-2	5.37	81.36	167.78	-0.0	-0.0	-0.0	41.06	295.57
0-1	9.64	55.83	142.82	-0.0	-0.0	-0.0	36.27	244.56
1-2	0.0	25.54	24.95	-0.0	-0.0	-0.0	4.79	55.28
2-5	10.52	5.64	94.80	-0.0	-0.0	-0.0	5.50	116.46

DISAPPEARANCE:

0-2	0.0	58.95	94.01	-0.0	-0.0	-0.0	0.0	152.96
0-1	0.0	40.44	62.53	-0.0	-0.0	-0.0	0.0	102.97
1-2	4.26	18.52	31.48	-0.0	-0.0	-0.0	0.0	54.26
2-5	16.19	0.0	106.23	-0.0	-0.0	-0.0	0.0	122.42

INSTALLATION: 2 HORIZON: 2

PRODUCTION:

CLASS	16.MAY	-25.JUN	-12.AUG	-04.OCT	-23.NOV	-04.FEB	-25.MAR	-14.MAY	TOTAL
0-2	0.0	0.0	123.99	-0.0	-0.0	-0.0	217.20		341.19
0-1	0.0	0.0	115.84	-0.0	-0.0	-0.0	166.37		282.21
1-2	2.56	0.0	8.14	-0.0	-0.0	-0.0	50.83		61.53
2-5	0.0	0.0	126.03	-0.0	-0.0	-0.0	0.0		126.03

MORTALITY:

0-2	37.91	124.16	201.34	-0.0	-0.0	-0.0	0.0	363.41
0-1	40.47	80.58	195.88	-0.0	-0.0	-0.0	0.0	316.94
1-2	0.0	43.56	5.46	-0.0	-0.0	-0.0	0.0	49.02
2-5	39.07	64.95	29.48	-0.0	-0.0	-0.0	72.29	205.79

DISAPPEARANCE:

0-2	96.31	62.59	0.0	-0.0	-0.0	-0.0	174.55	333.45
0-1	91.67	33.18	0.0	-0.0	-0.0	-0.0	156.52	281.37
1-2	7.20	29.40	0.0	-0.0	-0.0	-0.0	18.03	54.63
2-5	102.21	84.51	0.0	-0.0	-0.0	-0.0	87.26	273.98

APPENDIX 5

Fine root production and mortality estimates (g/m^2) based on three computational methods and four types of groupings of fine root data. See Section 4.4.1. for an explanation of the different computational methods.

DECISION MATRIX

INST	PROD		MORT	
2	514.	814.	490.	789.
	567.	822.	542.	798.
5	112.	156.	215.	259.
	149.	210.	251.	313.
16	287.	321.	356.	390.
	316.	364.	385.	433.
71	199.	217.	378.	395.
	318.	324.	496.	502.
72	208.	292.	218.	302.
	212.	286.	222.	296.

PERCENTAGE OF TYPE 1

INST	PROD		MORT	
2	100.	158.	100.	161.
	110.	160.	111.	163.
5	100.	140.	100.	121.
	133.	187.	117.	146.
16	100.	112.	100.	110.
	110.	127.	108.	122.
71	100.	109.	100.	105.
	160.	162.	131.	133.
72	100.	140.	100.	139.
	102.	138.	102.	136.

ALL CHANGES

INST	PROD		MORT	
2	512.	579.	487.	554.
	512.	591.	487.	566.
5	112.	127.	215.	230.
	122.	158.	225.	261.
16	242.	254.	311.	323.
	253.	259.	322.	328.
71	118.	118.	296.	296.
	139.	162.	318.	341.
72	168.	166.	178.	176.
	168.	169.	178.	179.

PERCENTAGE OF TYPE 1

INST	PROD		MORT	
2	100.	113.	100.	114.
	100.	115.	100.	116.
5	100.	113.	100.	107.
	109.	141.	105.	121.
16	100.	105.	100.	104.
	105.	107.	104.	106.
71	100.	100.	100.	100.
	118.	137.	107.	115.
72	100.	99.	100.	99.
	100.	101.	100.	101.

SIGNIFICANT CHANGES
ALPHA = 0.050

INST	PROD		MORT	
2	481.	576.	487.	489.
	481.	563.	487.	487.
5	112.	106.	215.	230.
	101.	78.	225.	246.
16	242.	242.	311.	323.
	242.	215.	322.	328.
71	118.	34.	296.	296.
	105.	33.	318.	284.
72	168.	158.	178.	164.
	168.	150.	178.	163.

PERCENTAGE OF TYPE 1

INST	PROD		MORT	
2	100.	120.	100.	100.
	100.	117.	100.	100.
5	100.	95.	100.	107.
	90.	70.	105.	114.
16	100.	100.	100.	104.
	100.	89.	104.	106.
71	100.	28.	100.	100.
	89.	28.	107.	96.
72	100.	94.	100.	92.
	100.	89.	100.	91.

APPENDIX 6

List of understory plant species in the five stands.

STAND A:
INSTALLATION 71 PLOT 14

Gaultheria shallon
Mahonia nervosa
Vaccinium parvifolium
Vaccinium ovalifolium
Rosa gymnocarpa
Rubus ursinus
Rubus parviflorus
Symphoricarpos albus

Achlys triphylla
Pteridium aquilinum
Blechnum spicant
Mycelis muralis
Linnaea borealis
Fragaria spp.
Adenocaulon bicolor
Viola spp.
Hieracium albiflorum
Galium triflorum
Chimaphila umbellata

Kindbergia oregana
Dicranum scoparium
Hylocomium splendens
Plagiothecium undulatum
Rhytidiadelphus loreus
Rhytidiadelphus triquetrus
Rhytidiopsis robusta
Pleurozium schreberi
Trachebrium spp.
Isothecium stoloniferum

STAND B:
INSTALLATION 2 PLOT 6

Gaultheria shallon
Mahonia nervosa
Rosa gymnocarpa
Rubus ursinus

Achlys triphylla
Pteridium aquilinum
Linnaea borealis

Kindbergia oregana
Dicranum scoparium
Hylocomium splendens
Rhytidiopsis robusta

STAND C:
INSTALLATION 5 PLOT 10

Gaultheria shallon
Vaccinium parvifolium
Rubus ursinus
Rubus spectabilis
Ribes lacustre

Achlys triphylla
Pteridium aquilinum
Polystichum munitum
Mycelis muralis
Linnaea borealis
Fragaria spp.
Viola spp.
Galium triflorum
Pyrola secunda
Orthilia secunda

Kindbergia oregana
Hylocomium splendens
Rhytidiadelphus loreus
Rhytidiadelphus triquetrus
Rhytidiopsis robusta
Polytrichum juniperinum
Plagiomnium insigne

STAND D:
INSTALLATION 16 PLOT 2

Gaultheria shallon
Mahonia nervosa
Vaccinium parvifolium
Rosa gymnocarpa
Rubus ursinus
Symphoricarpos albus
Amelanchier alnifolia

Achlys triphylla
Polystichum munitum
Blechnum spicant
Mycelis muralis
Linnaea borealis
Fragaria spp.
Viola spp.
Hieracium albiflorum
Galium triflorum

Kindbergia oregana
Dicranum scoparium
Hylocomium splendens
Plagiothecium undulatum
Rhytidiadelphus loreus
Rhytidiadelphus triquetrus
Rhytidiopsis robusta
Rhizomnium glabrescens
Trachebrium spp.
Isothecium stoloniferum
Polytrichum juniperinum

Kindbergia oregana
Dicranum spp.
Hylocomium splendens
Rhytidiadelphus loreus
Rhytidiopsis robusta
Rhizomnium glabrescens

STAND E:
INSTALLATION 72 PLOT 14

Mahonia nervosa
Vaccinium parvifolium

Achlys triphylla
Pteridium aquilinum
Polystichum munitum
Blechnum spicant
Dryopteris expansa
Mycelis muralis
Linnaea borealis
Adenocaulon bicolor
Viola spp.
Galium triflorum
Tiarella trifoliata
Tiarella laciniata
Trientalis latifolia
Campanula scouleri